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INTRODUCTION

Our Furry Friends

THE KITTEN LOITERING OUTSIDE MY LOCAL FIREHOUSE WAS STILL THERE TWO HOURS LATER, yowling with hunger, when the community council meeting I was attending broke up. "Will you take him home?" asked my neighbor. "My friend Steve wants to adopt a cat, so it would just be for one night." Of course, I would. But the next day I learned Steve wanted a tabby, and this kitten had a coat as soft as a rabbit's but no stripes. Your loss, Steve. Bunny Boy, now 12 years old and still with me, is my favorite cat ever. That's saying a lot, considering how many pets have shared my home over the years.

At the moment, my husband and I have three cats and two dogs, and I consider myself a cat person *and* a dog person. There are no hard-and-fast rules, though, about what makes someone a typical owner of either species, as "What Your Pet Reveals about You" (*page 11*) explains. In fact, cats and dogs often come into our lives in unexpected ways. They also come in all shapes and shades—a reflection of how their evolution has been affected by human contact, a process described in "From Wolf to Dog" (*page 28*) and "The Taming of the Cat" (*page 64*).

When I was a college student majoring in biology more than 30 years ago, ascribing human emotions and motives to animals—anthropomorphism—was frowned on. Today, though, many scientists feel comfortable saying what we pet owners have known all along: that animals *feel* things. Even rats have empathy for their cage mates, and creatures of many species apparently grieve over the loss of relatives or close companions—as we learn in "Do Animals Feel Empathy?" (*page 92*) and "When Animals Mourn" (*page 100*). Yet recent research highlighted in "The World According to Dogs" (*page 38*) also shows that pet owners often misinterpret their charges' feelings.

Pets fill our own emotional need to nurture other living things, making us healthier and happier, according to "Pets: Why Do We Have Them?" (*page 6*). Canine companions may even help in the effort to cure cancer, as described in "Cancer Clues from Pet Dogs" (*page 54*). Indoor cats, meanwhile, might not deserve the bad rap they're getting for spreading a brain-altering parasite to humans—a surprise reported in "Played by a Parasite" (*page 84*).

More than half of American households have a pet—usually more than one and often considered members of the family. They bring us joy, occasional sadness (if only because their lives are measured in dog years) and now an unending source of viral videos. Read on to learn why dogs and cats behave the way they do and what makes the human-pet bond so strong.

Dawn Stover
Issue Editor
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THE SCIENCE OF DOGS AND CATS

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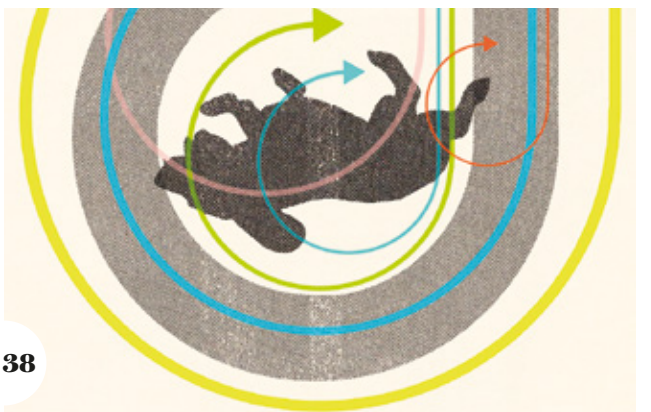

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For the Love of Pets

THE SCIENCE OF DOGS AND CATS

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Illustration by Bomboland

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Pets:

Why Do We Have Them?

THE SCIENCE OF DOGS AND CATS

People have an innate interest in other species, but we like having pets for a variety of social reasons

By Daisy Yuhas

IN BRIEF

Both innate fascination and cultural norms influence the human tendency to adopt companion animals. **Human-animal bonds** can be powerful sources of social support, although the extent of that support depends on the strength of the bond with the animal. **Reports from owners** suggest that having pets makes people happier and gives their lives meaning. Studying how people relate to their pets offers a window into human needs and desires.

GETTY IMAGES

Illustrations by Shaw Nielsen

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On my 10th birthday, I got a puppy. I was so shocked—I had wanted a dog for as long as I could remember—and so overwhelmed with happiness that I burst into tears. For the next 14 years, Happy, a beagle, charmed everyone he met. And when he passed, all of us who had known him mourned, as we would for any loved one. More than half of American households have a pet—that is, an animal kept primarily for companionship. And despite the fact that these housemates may bear scales, fur, fins or feathers, people often view their animals as family members. In 2014 we spent an estimated $58 billion on our animal companions and untold hours caring for them.

For 50 years psychologists have been trying to unravel the appeals of animal companionship in hopes of deciphering just why we invest so much in these creatures. In the process, anthrozoologists—scientists who study human-animal relationships—have discovered a window into human sociality more broadly. Our interactions with animals can be useful models for understanding how issues of identity, nurturing, support and attachment play out in a relationship. "It's all about human psychology," says anthrozoologist Pauleen Bennett of La Trobe University in Australia. "Pets help us fill our need for social connectedness."

Although the motivations for pet ownership may vary as much as a golden retriever and a goldfish, scientists are finding that some common threads tie people to their household pets. Our attraction to animals may be subconscious, driven by biological and social forces that we do not fully acknowledge. In addition, the emotional bond between pets and their owners can bring varied benefits, from lowered stress to novel adventures. The more we uncover about our companion animals, the more we may learn about our human attachments as well.

INBORN ATTRACTION?

Part of our attraction to animal companionship is innate. In 2013 psychologist Vanessa LoBue of Rutgers University and her colleagues revealed that toddlers one to three years old spend more time interacting with live animals—whether fish, hamsters, snakes, spiders or geckos—than they do with inanimate toys when given a choice between the two.

Humans even have specialized brain cells for recognizing animal life. Researchers led by Christof Koch of the Allen Institute for Brain Science in Seattle (he also serves on *Scientific American Mind*'s board of advisers) have found neurons in the amygdala, an area involved in emotions, that respond preferentially to animal images. The 2011 finding hints at a neural basis for the powerful emotional reactions animals elicit from us.

Many animals seem to tap into humans' attraction to the adorable, a drive that also may motivate good parenting. Behavioral researchers have long noticed that humans seem to have inborn, positive responses to beings with characteristics typical of human infants—such as wide eyes, broad foreheads and large head-to-body ratios.

To better understand the responses that cuteness can elicit, psychologist Hiroshi Nittono and his colleagues at Hiroshima University in Japan published a series of experiments in 2012 in which college students, 132 in all, searched for a digit in numerical matrices or lifted tiny objects from small holes using tweezers. Afterward, participants viewed a series of photographs before attempting the attention or motor task for a second time.

Nittono and his colleagues found that students who viewed adult animals or food—stimuli they had rated as pleasant but not cute—did not improve between trials. But the students who saw cute baby animals did the tweezer task faster and more dexterously and performed the visual search task faster the second time, suggesting that being exposed to such creatures motivates focused, attentive behavior. This finding suggests that humans are primed to attend to fragile, young infants, who may require greater care than other beings. Clearly, baby animals exploit the same instinctive responses in us that human infants elicit.

Such findings lend credence to the idea that our interest in pets stems from what biologist E. O. Wilson has called "biophilia," or an inherent tendency to focus on life and lifelike processes. Our fascination with all manner of fauna might explain why people adopt such a wide range of animal life, from tarantulas to salamanders.

Yet Wilson has also acknowledged that our interest in animals depends on personal and cultural experience. For example, dogs are popular in many Western countries but are considered unclean in traditional Islamic communities. Indeed, psychologist Harold A. Herzog of Western Carolina University has argued that pet

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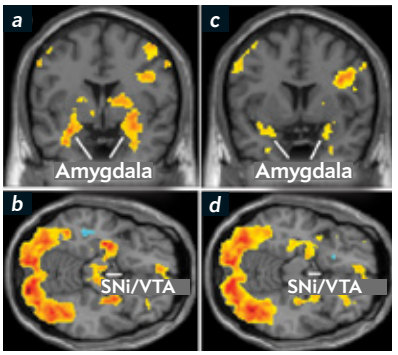
BRAIN IMAGING



Massachusetts General Hospital researchers discovered that similar brain regions, including the amygdala, engage when women view their own children (*a*, *b*) and dogs (*c*, *d*). The overlap is not absolute, however. Certain midbrain areas (SNi/VTA) activate only when mothers see their kids.

Our interest in other animals may be partially innate. Children are fascinated by diverse creatures from a young age.

Some researchers think we are drawn to cute animals because aspects of their appearance, such as large eyes and soft contours, somewhat resemble a human infant's features.

keeping is driven principally by culture. In a paper published in 2013 Herzog and his colleagues assessed the fluctuating popularity of dog breeds using the American Kennel Club's registry from 1926 to 2005. They found no relationship between a breed's health, longevity or behavioral traits such as aggressiveness or trainability and its popularity. Instead, they argued, the trends in top dogs were erratic and seemed to shift suddenly, as if driven by fashion. In 2014 three of the authors, including Herzog, further discovered that movies featuring specific dog breeds would boost that pooch's popularity for up to a decade. In the 10 years following the 1963 release of *The Incredible Journey,* starring a Labrador retriever, people registered Labs in the kennel club at an average rate of 2,223 dogs a year, in contrast to 452 dogs a year in the previous decade.

Extending these findings to other species, Herzog posited that people may keep pets simply because other people keep pets, reflecting our penchant for imitation. He pointed to a brief craze in the U.S. for turtle keeping, a koi fish fad in Japan and what he jokingly identified as a brief "epidemic of Irish setters" as further evidence.

FRIENDS WITH BENEFITS

BUT EVEN IF IMITATION plays a role in their choices, most people profess to wanting pets for companionship. This friendship then sustains the connection despite the costs of ownership. Indeed, some animal-human relationships feel similar in certain ways to human relationships. In a study published in 2014 Massachusetts General Hospital veterinarian Lori Palley and her colleagues used functional magnetic resonance imaging to measure brain activity in 14 mothers while they were looking at pictures of their children or their dogs or at pictures of other people's children or unfamiliar dogs. The researchers found that the brain activation patterns evoked by images of the women's own children and dogs were very similar and that those patterns were distinct from those elicited by unknown children and canines, suggesting that maternal feelings may extend to animals. Pets may thus help fill a human need to nurture other living beings.

An animal also can be on the flip side of this relationship, serving as a source of comfort. In the 1960s Yeshiva University child psychologist Boris Levinson observed that troubled, socially withdrawn children became talkative and enthusiastic about therapy when his dog, Jingles, was present during a session. This observation spurred a series of investigations into whether or not keeping pets could improve well-being. In a 1980 study of 92 people, biologist Erika Friedmann of the University of Pennsylvania reported that pet owners were more likely to be alive a

FROM "PATTERNS OF BRAIN ACTIVATION WHEN MOTHERS VIEW THEIR OWN CHILD AND DOG: AN FMRI STUDY," BY LUKE E. STOECKEL ET AL., IN *PLOS ONE*, VOL. 9, NO. 10, ARTICLE NO. E107205; OCTOBER 3, 2014 (*brain imaging*); ADIE BUSH *Aurora Photos* (*child with pony*); GETTY IMAGES (*toddler and puppy*)

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THE RESEARCHERS FOUND THAT PEOPLE WHO FREQUENTLY KISSED THEIR DOGS HAD HIGHER LEVELS OF THE BONDING HORMONE OXYTOCIN.

year after a heart attack than were people who did not have a companion animal—possibly because the animals afforded some form of stress relief. Yet efforts to replicate such findings have had mixed results, and animal-assisted therapy, the field that Levinson's work inspired, has been criticized for overstating the ability of animals to ameliorate mental illness [see "Can Animals Aid Therapy?" by Scott O. Lilienfeld and Hal Arkowitz, on page 24].

Nevertheless, some people may gain psychological support from their pets and keep them for exactly this reason. In a study published in 2012 psychologist Sigal Zilcha-Mano, then at the Baruch Ivcher School of Psychology at the Interdisciplinary Center Herzliya in Israel, and her colleagues asked 285 cat or dog owners to answer a questionnaire assessing their emotional connection with their pet. Then the researchers asked 120 of these pet owners to take a challenging word test. By recording her subjects' blood pressure—a measure of stress—during the test, Zilcha-Mano found that individuals who had their pet present or thought about the pet before taking the test had lower stress than people who had no contact with the pet. Yet the strength of this benefit depended on how attached the owner was to his or her pet. In other words, the level of emotional sustenance a pet owner receives depends on how close he or she feels to the animal.

Different hormonal cocktails seem to underpin various degrees of animal-human attachment. In a study published in 2012 biologist Linda Handlin of the University of Skövde in Sweden and her colleagues measured levels of the bonding hormone oxytocin and stress hormone cortisol in 10 owners of female Labrador retrievers and correlated the results with self-reported data about the owners' relationships with their dogs. Owners who had higher oxytocin levels and lower cortisol levels when interacting with their dogs tended to have closer bonds with their pets. People who frequently kissed their dogs, for example, had higher levels of oxytocin, and women who reported that they dreaded their dog's death had lower cortisol levels, perhaps because they rely on their animals for stress relief.

A person's social orientation could also factor into the strength of the pet-person tie. In a study published in 2012 psychologist Andrea Beetz of the University of Rostock in Germany and her colleagues asked 47 seven- to 11-year-old boys who had difficulties forming social attachments to present a story before a committee of unfamiliar adults and then take a math test. During this ordeal, 24 of the children were accompanied by a dog, 10 had a friendly human by their side and the others had a toy dog nearby.

Beetz found that children accompanied by a real dog had the lowest cortisol levels and that those with human company had the highest, probably because people made these boys nervous. Furthermore, among those boys who benefited from the dog, those who engaged in the most petting and other physical contact with the dog during the test showed the least stress, as measured by salivary cortisol. Thus, interacting with animals may be an especially good buffer against stress for those who find human social interaction difficult. "Some things are much easier with animals," Beetz says. "They are easier to forgive, don't talk back, and there's less inhibition when it comes to physical contact."

ANIMAL ANTICS

YET PETS ARE MUCH MORE than human substitutes. Many people with no obvious social deficits reap varied psychological benefits from owning a pet. In 2012 Bennett presented preliminary findings from a student, psychologist Jordan Schaan, then at Monash University in Australia, who had interviewed 37 dog owners who were personally and professionally successful and had an above-average connection to their animals. (The subjects were

GALLERY STOCK

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educated and affluent and had fulfilling romantic partnerships, for instance.) Among the benefits of dog ownership that these individuals reported were amusement—the animals' antics made their owners laugh—a sense of meaning from having responsibility for the welfare of another living thing, and an entrée into new experiences and relationships: a puppy can be a great way to meet neighbors.

Furthermore, many pet owners described their companion animals as instructors in a simpler, more virtuous lifestyle. Bennett and Schaan discovered that their highly successful subjects actually looked to their dogs as role models for a better life. People felt they could derive unconditional love and forgiveness from their dogs, whereas human beings seemed more likely to disappoint one another. "There's something about animals that's very genuine and honest," Bennett says. "We miss that in our human interactions."

Bennett and other anthrozoologists acknowledge that owners project some of this dynamic onto their animals. An owner can "read" a response into an animal companion's behavior regardless of the animal's intentions. Yet such projections are precisely what make this field ripe for psychology: they reveal our own social needs and desires. Animal relationships may someday provide useful comparison points to human connections—a benchmark for investigating empathy, caring and even decision making. That these creatures can fit many molds while being so different from us makes these friendships uniquely valuable.

The study of animal companionship is still in its infancy. But without this research, we could not begin to fathom the rich and varied range of relationships that make up human experience. SA

Daisy Yuhas is an associate editor at *Scientific American Mind*.

MORE TO EXPLORE

Pets in the Family: An Evolutionary Perspective. James A. Serpell and Elizabeth S. Paul in *The Oxford Handbook of Evolutionary Family Psychology*. Edited by Todd K. Shackelford and Catherine A. Salmon. Oxford University Press, 2011.

Biology, Culture, and the Origins of Pet-Keeping. Harold A. Herzog in *Animal Behavior and Cognition*, Vol. 1, No. 3, pages 269–308; August 2014.

Toward a Psychology of Human-Animal Relations. Catherine E. Amiot and Brock Bastian in *Psychological Bulletin*, Vol. 141, No. 1, pages 6–47; January 2015.

FINDINGS

What Your Pet Reveals about You

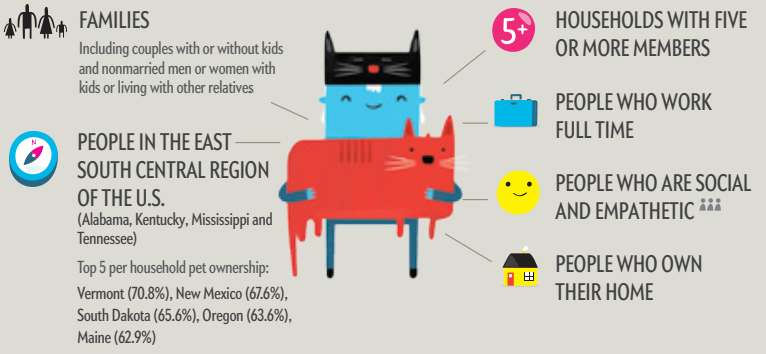
Is there a typical cat person or snake owner? The jury is still out

By Karen Schrock Simring

Most of us think our pets say a lot about who we are. Why else would we proudly proclaim our loyalty on T-shirts and in online profile pictures? Yet few scientists have rigorously investigated whether our choice of pet reveals anything about our personality, beliefs or lifestyle. SCIENTIFIC AMERICAN MIND rounded up the smattering of available research and highlighted some of the more interesting findings in the infographic that starts below and continues on the next pages. Some information comes from peer-reviewed studies, but the bulk of the data derives from huge market surveys undertaken by interested parties in the pet industry, such as the American Veterinary Medical Association, which tracks pet populations, owner demographics and expenditures to follow how pet ownership in the U.S. changes over time. As you will see, these surveys reveal interesting things about people and the pets they love.

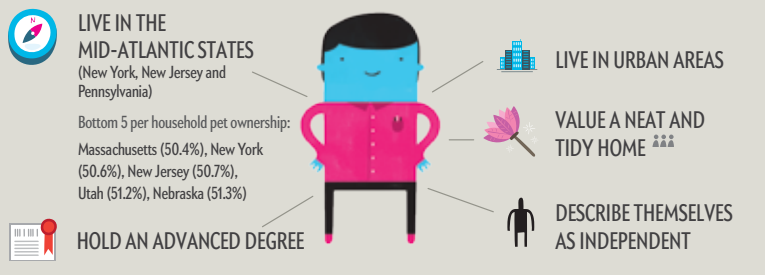
Karen Schrock Simring is a contributing editor for *Scientific American Mind*.

PET OWNERSHIP IS HIGHEST AMONG:


FAMILIES
Including couples with or without kids and nonmarried men or women with kids or living with other relatives
PEOPLE IN THE EAST SOUTH CENTRAL REGION OF THE U.S.
(Alabama, Kentucky, Mississippi and Tennessee)
Top 5 per household pet ownership:
Vermont (70.8%), New Mexico (67.6%), South Dakota (65.6%), Oregon (63.6%), Maine (62.9%)
5+
HOUSEHOLDS WITH FIVE OR MORE MEMBERS
PEOPLE WHO WORK FULL TIME
PEOPLE WHO ARE SOCIAL AND EMPATHETIC
PEOPLE WHO OWN THEIR HOME

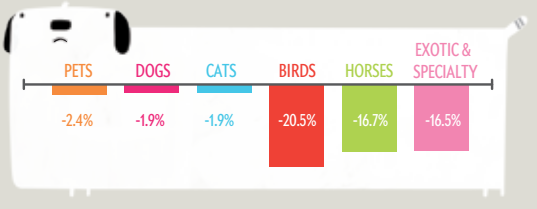
FUN STAT: For every type of pet, in 8 out of 10 households the primary caretaker of the pet is female.

PEOPLE WHO DO NOT OWN PETS ARE MORE LIKELY THAN PET OWNERS TO:


LIVE IN THE MID-ATLANTIC STATES
(New York, New Jersey and Pennsylvania)
Bottom 5 per household pet ownership:
Massachusetts (50.4%), New York (50.6%), New Jersey (50.7%), Utah (51.2%), Nebraska (51.3%)
HOLD AN ADVANCED DEGREE
LIVE IN URBAN AREAS
VALUE A NEAT AND TIDY HOME
DESCRIBE THEMSELVES AS INDEPENDENT

PET OWNERSHIP IS DECREASING

Since 2006, the percentage of U.S. households that own a pet has declined by 2.4 percent; experts blame the recession.



Indicates a finding from a peer-reviewed paper.

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What Your Pet Reveals about You

IF YOU HAVE A DOG, YOU'RE MORE LIKELY TO:

BE IN SENIOR MANAGEMENT
(COMPARED WITH OTHER PET OWNERS)

CONSIDER YOUR PET PART OF THE FAMILY
(COMPARED WITH OTHER PET OWNERS)

- Live with family members
  (COMPARED WITH THE GENERAL POPULATION)
- Not have a college degree
  (COMPARED WITH PEOPLE WHO DO NOT OWN DOGS)
- Be a professor, nurse, information technology professional, military professional or entertainer
  (COMPARED WITH OTHER PET OWNERS WHO WORK FULL TIME)
- Be extroverted, agreeable and conscientious ⁂
  (COMPARED WITH CAT OWNERS)
- Have gotten the dog from a shelter or rescue group
  (COMPARED WITH ANY OTHER SOURCE)
- Live in Arkansas, New Mexico, Kentucky, Missouri or West Virginia than in other states
  (BASED ON PER HOUSEHOLD OWNERSHIP)

IF YOU HAVE A CAT YOU'RE MORE LIKELY TO:

BE DIVORCED, WIDOWED OR SEPARATED
(COMPARED WITH OTHER PET OWNERS)

LIVE IN AN APARTMENT
(COMPARED WITH OTHER PET OWNERS)

- Be neurotic and open to new experiences ⁂
  (COMPARED WITH DOG OWNERS)
- Be college educated ⁂
  (COMPARED WITH PEOPLE WHO DO NOT OWN CATS)
- Be less socially dominant ⁂
  (COMPARED WITH OTHER PET OWNERS)
- Live in Vermont, Maine, Oregon, South Dakota, or Washington than in other states
  (BASED ON PER HOUSEHOLD OWNERSHIP)
- Be a physician, real estate agent, science or medical lab technician, machine operator or personal caretaker
  (COMPARED WITH OTHER PET OWNERS WHO WORK FULL TIME)

RABBIT OWNERS ARE THE MOST INTROVERTED AND NEUROTIC OF ALL PET OWNERS, ACCORDING TO ONE STUDY ⁂

⁂ Indicates a finding from a peer-reviewed paper.

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IF YOU HAVE A BIRD, YOU'RE MORE LIKELY TO:

BE UNEMPLOYED
(COMPARED WITH OTHER PET OWNERS)

DESCRIBE YOURSELF AS POLITE AND CARING ***
(COMPARED WITH HORSE, TURTLE AND SNAKE OWNERS)

Live in California, Oregon, Washington or Nevada
(BASED ON PER HOUSEHOLD OWNERSHIP)

Be socially dominant if you're female ***
(COMPARED WITH HORSE, TURTLE AND SNAKE OWNERS)

Be socially outgoing and expressive ***
(COMPARED WITH HORSE, TURTLE AND SNAKE OWNERS)

IF YOU HAVE A HORSE, YOU'RE MORE LIKELY TO:

Hold an advanced degree
(COMPARED WITH OTHER PET OWNERS)

Be more assertive and introspective and less warm and nurturing ***
(COMPARED WITH TURTLE, SNAKE AND BIRD OWNERS)

Be aggressive and socially dominant if you're male and nonaggressive and easygoing if you're female ***
(COMPARED WITH TURTLE, SNAKE AND BIRD OWNERS)

Be a homeowner
(COMPARED WITH OTHER PET OWNERS)

Live in Texas, Oklahoma, Arkansas or Louisiana
(BASED ON PER HOUSEHOLD OWNERSHIP)

Live in a rural area
(COMPARED WITH OTHER PET OWNERS)

BE MARRIED
(COMPARED WITH OTHER PET OWNERS)

IF YOU HAVE A COLD-BLOODED EXOTIC PET:

And are male, you are much less agreeable than female owners or male owners of traditional pets ***

And are female, you are much more open to new experiences than male owners or female owners of traditional pets ***

And it is a snake, you're more likely to ...

Describe yourself as more relaxed and unpredictable ***
(COMPARED WITH HORSE, TURTLE AND BIRD OWNERS)

Be unconventional and novelty-seeking ***
(COMPARED WITH HORSE, TURTLE AND BIRD OWNERS)

And it is a turtle, you're more likely to ...

Be hardworking, reliable and upwardly mobile ***
(COMPARED WITH HORSE, SNAKE AND BIRD OWNERS)

Describe yourself as more rational and goal-oriented ***
(COMPARED WITH HORSE, SNAKE AND BIRD OWNERS)

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And Now a Few Words from Pet Owners

Scientific American Mind recently asked its readers to weigh in on their own pet predilections. More than 2,000 people responded to the online survey, and some results differed quite a bit from the data shown on the preceding pages. This is not surprising. Big surveys of many thousands of pet owners will show, for instance, that dog owners (on average) are somewhat more extroverted than cat owners (on average), but the individual differences within each group are greater than the differences between them. Thus, there are plenty of boisterous cat owners and reserved dog owners. In addition, many people have more than one type of pet and cannot be strictly labeled as partial to one particular creature.

Our survey drives home the fact—supported by several studies—that our animal companions are integral to how we see ourselves. For instance, men who like being seen as tough may get a tough-looking dog to help them project that image. Some people are proud rabbit or poodle owners because having those pets is a family tradition. Other folks might keep less popular critters, such as spiders or snakes, because they feel these animals are misunderstood, much like themselves.

Below, at the left, we provide some intriguing findings from readers who admire or have more than one type of pet and some data on how owners of specific animals describe themselves. At the right is a sampling of the hundreds of passionate responses we got to the question: What makes you a dog person, a cat person, neither or both? Visit our Web site (www.ScientificAmerican.com/Mind/pet-survey) for more survey results. —*The Editors*

SURVEY RESULTS

Snake owners were the most likely of all pet owners to describe themselves as "neat and tidy" and, surprisingly, to consider their pet "part of the family."

Fish owners were the most likely to describe themselves as calm and emotionally stable.

Rabbit owners were the most likely to describe themselves as sympathetic and warm and open to new experiences.

Horse owners were the most likely to describe themselves as dependable and self-disciplined.

Hamster owners were the most likely to have an advanced degree.

Guinea pig owners were the least likely to describe themselves as extroverted.

Owners of unusual pets were more likely to have a menagerie. For instance, more than half of ferret owners said they had six or more pets. Dog owners, on the other hand, were the most likely to have just one animal.

More than half of cat owners described themselves as fond of both cats and dogs. But more than half of dog owners said they preferred only canines.

Beyond the 12 popular pets we asked about in our survey, our respondents reported keeping an astonishing variety of species, from chickens to exotic insects to sugar gliders, which are small possums (*right*). ▶

"I STARTED LIFE AS A DOG PERSON. THEN LATER IN LIFE A CAT CORRECTED MY ERROR."

"Dogs are living Buddhas—compassionate beings who live completely in the present moment."

"Even my pet rock is part of the family. We don't discriminate."

"I am impressed by how nearly wild—still functionally in touch with their instincts—cats are."

"My dogs and cats each feed a different part of my soul."

"When you finally win over a cat, it's so worth it."

"All single moms need a giant bearlike protector dog who is both 'scary' and loves to cuddle."

"I have PTSD. Cats help me with my hypervigilance because they pick up on things first. Petting them puts me at peace."

"Both dogs and cats are preferable to most humans."

CAROLYN A. MCKEONE/*Getty Images* (*sugar glider*); ISTOCKPHOTO (*speech bubbles and animal icons*)

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The Science of a Friendship

Why dogs fit into families so well

By Ádám Miklósi

Illustrations by Shaw Nielsen

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AT A RESEARCH INSTITUTE IN HUNGARY NOT FAR FROM THE BANKS OF THE DANUBE, an emotional bond began to grow between an elderly night janitor and an old watchdog living there named Balthasar. The dog would sometimes spend the day at the janitor's home. "Unfortunately, this relationship lasted only a few months, because the janitor became ill … and eventually died," writes animal behaviorist Vilmos Csányi, founder of the department of ethology at Eötvös Loránd University in Budapest, in his book *If Dogs Could Talk*. Shortly after the janitor's death, researchers at the institute noticed that Balthasar would disappear from time to time, particularly in the mornings. "We tracked down what he was doing during his absences," Csányi reports, "and found that he would cross the busy highway, go to his adoptive master's old house in the village, and sit in front of it for hours."

Relationships between people and dogs have spawned a myriad of fascinating stories, not least because the association is so improbable. Just take a look at your dog or at any dog in your neighborhood. Would you expect these creatures to be humanity's best friends? They look very different from us. They behave very differently. They do not seem to have an affinity for culture. And they cannot speak a single word. Yet most people in Western cultures regard their dogs as members of the family in the truest sense. And now behavioral science is starting to reveal how this unlikely friendship came to be.

Fewer than 20 years have passed since scientific teams led by psychologist Michael Tomasello of the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, and Csányi in Budapest independently published research papers on how family dogs can follow human pointing gestures to find hidden food. That work marked the birth of a flourishing field of investigation into the biological foundations of the human-dog bond. Since then, researchers have learned that humans and their dog companions live in an attachment relationship, just like mothers and infants. They enjoy one another's company and find mutual support in potentially challenging circumstances. Attachment relationships also provide the foundation of cooperation: humans help dogs navigate modern society; dogs, in return, help us when we lack a specific ability, such as sight. And when dogs are treated poorly, they sometimes show the same psychological symptoms of an attachment gone wrong that children do.

Research has also shown that dogs have been able to adjust smoothly to

IN BRIEF

Dogs' social competence has helped them join the human family. Domestication has shaped the development of their communication and learning skills, making them sensitive to human behavior if they are reared in an appropriate social environment. **An attachment relationship** forms the social basis of human-dog collaborations. The strong bond also facilitates behavioral and emotional synchronization. **Dogs excel** in their flexible social behavior and have an incredible ability to learn from observations, but only if humans invest the necessary time and effort in their relationship.

PRECEDING PAGE AND OPPOSITE PAGE: GETTY IMAGES

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The sensitivity of dogs to human emotions means they might also experience stress when their owner is crying.

family life because of their attentiveness and their sensitivity to human modes of communication and emotional behavior. Dogs tend to express their emotions through vocalization, just as humans do, and they seem to react to the emotional nuances of human speech and cries. Dogs can put on displays of behavior with the canniness of any adolescent to elicit a desired response from their owner. They also excel in learning from humans through observation, which allows them to follow the rules of the family.

Now modern technology is extending the human-dog relationship, both by helping us to understand it better and by enabling different forms of interaction. Images of brain activity in humans and dogs show striking parallels in how each species encodes the emotional content of the other's vocalizations. And devices ranging from state-of-the-art sensors to interactive robots may one day let dogs participate in new cooperative tasks with humans. As we move into an ever more complex future, the ability of dogs to attach and adapt should keep them close by our side.

FITTING IN

DOGS ARE UNIQUE in the animal kingdom because they have figured out how to join the community of an entirely alien species—evidence of sophisticated social competence. Psychologists define social competence as the ability of individuals to harmonize their needs and expectations with those of the collective, letting them fit in with the group. Social competence depends on mastering a set of skills, including the abilities to form attachments, regulate aggression, learn and follow rules, provide assistance and participate in various group activities.

Social competence also comes into play when members of a nonhuman species join our social units. So when I design studies of the human-dog relationship with my group at Eötvös Loránd, we focus on the ability of dogs to exhibit each of the components of social competence. In this way, we come to understand their compatibility with us. But a noteworthy question is how dogs were able to develop this competence in the first place.

Anybody who has had the luck or misfortune to raise wolves and dogs at home would agree that the difference between the two is a big one. Wolves do not easily become members of the family, despite all efforts to socialize them to human life. Dogs have been able to bridge the divide because of significant changes in their genes over centuries of domestication, marked by the selection of genetic components that support the development of

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humanlike social competence when dogs are raised among people.

ATTACHMENT FOR LIFE

A CRUCIAL COMPONENT of social competence is the ability to form an attachment. Most researchers agree that the attachment between juvenile and adult dogs and their owners closely resembles the bond that exists between mothers and very young children. In the 1960s psychologists John Bowlby of the Tavistock Clinic in London and Mary Ainsworth, then at Johns Hopkins University, developed an intriguing theory to explain the strong tie between mothers and their babies. They argued that this bond, known as attachment, ensures that the baby develops in a safe environment with opportunities to explore and learn about the complexities of human life.

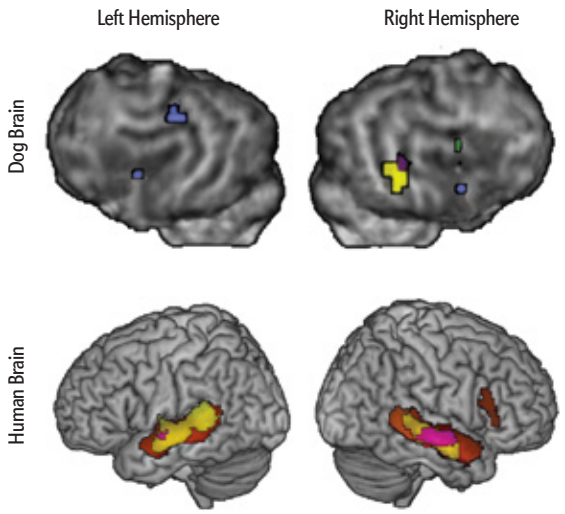
NEURAL IMAGING

Parallel Brains

Researchers of the human-canine bond have long wanted to see how a dog's brain reacts to human emotional signals. But the main tool for investigating neural activity—functional magnetic resonance imaging—requires a subject to lie completely still for several minutes. Within the past several years dogs became the first nonhuman species to learn to lie motionless in the apparatus without being physically restrained. On the strength of this breakthrough, last year neurobiologist Attila Andics of the MTA-ELTE Comparative Ethology Research Group in Budapest and his colleagues performed a comparative imaging study of humans and dogs to investigate whether canine and human brains process nonlinguistic acoustic stimuli in a similar way.

Andics's team recorded more than 100 vocalizations by humans and dogs and asked humans to judge the negative or positive emotional content of the sounds. Twenty-two people and 11 specially trained dogs listened to a long sequence of excerpts from these recordings while their brain activity was recorded. Even though the canine brain is much smaller than the human one, the researchers were able to locate two neural areas that performed similar functions in both species. One area was mostly active when the subjects listened to vocalizations of their own species independent of the emotional content of the voice, showing that dogs and humans each have a brain area in about the same location dedicated to this function.

Even more intriguing was the finding on the processing of emotional information—that human and canine brains have analogous regions where activity correlates with increasingly positive emotional content regardless of the species that produces the sounds. Although these brain areas process acoustic stimuli at a relatively basic level (related, for example, to the length and frequency of the vocalizations), the results provide a preliminary hint of the existence of a neural basis for why family dogs (and sensitive owners) may react so strongly to their companion's emotions. —*A.M.*



Imaging studies have shown that, like humans, dogs have specialized brain regions that process sounds of their own species (*shown as red in humans and blue in dogs*). We also both have regions that process sounds with positive emotional content (*yellow for humans; purple for dogs*). Note the overlap of yellow and purple regions, showing that in each brain, the same region lights up in response to positive vocalizations of either species.

FROM "VOICE-SENSITIVE REGIONS IN THE DOG AND HUMAN BRAIN ARE REVEALED BY COMPARATIVE FMRI," BY ATTILA ANDICS ET AL., IN *CURRENT BIOLOGY*, VOL. 24, NO. 5; MARCH 3, 2014 (*brain imaging*); DEPARTMENT OF ETHOLOGY, EÖTVÖS LORAND UNIVERSITY (*dog in fMRI scanner*)

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Ainsworth and her colleagues introduced a simple test that is now the standard method for measuring the quality of this bond in everyday life. Mothers and babies of around 12 to 18 months in age were observed in a series of settings in which the baby was exposed to a strange female or separated from the mother for short periods. The study showed that the babies regarded their mother as a safe base, returning to her from time to time. They also approached her for consolation after being left alone.

It took ethologists many years to recognize that dogs and their owners show this attachment pattern, too. In 1998 animal behaviorist József Topál and his colleagues at Eötvös Loránd asked 51 dog owners to participate in an experiment much like the study of mothers and their babies. The owner and dog were brought to an unfamiliar room and spent some time playing together, first just with each other, then with a toy offered by the owner. Next a friendly stranger entered. The owner left, and the dog spent some time either alone or in the company of the stranger. Somewhat to the surprise of the researchers, most of the dogs behaved like human infants. When the owners were present, the dogs stayed near them and did not attempt to leave the room. Most of the dogs also played readily with their owner. They played less with the stranger, and most stopped playing with the stranger when their owner left. The researchers interpreted this preference as an indication that the dog regarded the owner as a safe refuge in case of potential danger, as attachment theory would predict.

Topál's team then set out to test whether this behavior represents an attachment relationship with a comparative study of juvenile dogs and wolves. In this experiment, 13 wolves and 11 dogs were separated from their mothers within four to six days of birth and raised by humans until they were four months old. The researchers then conducted the experiment of the stranger and the toy. Despite having the same social experience as the dogs, the wolves did not differentiate between their owner and the stranger, and only dogs used their owner as a secure base. In a parallel study in 2001 animal behaviorist Márta Gácsi of Eötvös Loránd discovered that even adult dogs could develop an attachment relationship with humans, as when an older dog is rescued from a shelter. (As head of the group, I was also on the team for this study and all of the others conducted at Eötvös Loránd.) Thus, the ability to form an attachment relationship with humans is lifelong.

LIKE HUMANS, DOGS TEND TO EXPRESS EMOTIONS THROUGH VOCALIZATION, AND THEY SEEM TO REACT TO THE EMOTIONAL NUANCES OF HUMAN SPEECH AND CRIES.

FOR BETTER OR FOR WORSE

THE PROPENSITY that dogs show for attachment leaves their relationships with us open to some familiar, humanlike dysfunctions, especially for pets of city-dwelling people. Dogs that a century ago would have had the freedom to wander off and encounter people and other dogs are now often confined to apartments, lonely and with few opportunities to enjoy their time. Most people do well at socializing their dogs, perhaps even without knowing it. But when the owners are neglectful, their dogs, just like infants, are prone to develop separation anxiety. When left alone, these dogs bark excessively, try to escape by destroying walls and doors, and defecate and urinate on the floor.

A 2011 study of this phenomenon conducted by ethologist Veronika Konok and her colleagues at Eötvös Loránd found that when separated from their owner, most dogs stay close to the chair where the owner usually sits. In contrast, dogs displaying signs of separation anxiety do not show a preference for objects touched or left behind by their owner. The researchers concluded that these dogs might have problems associating their owner with his or her home or possessions, so the dogs do not feel safe when their owner is absent.

And just as with distressed infants, anxiety in canines is often an outcome of their caregiver's personality. In a study

GETTY IMAGES

Dogs that disobey rules—by stealing food, say—may appear guilty to their owners but are more likely fearful of punishment.

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Helping tend the flock has long been a canine practical specialty; a modern equivalent is assisting people with physical disabilities.

published in the journal *PLOS ONE* in 2015, Konok and her colleagues reported that owners who show greater degrees of avoidance in their human attachment relationships (say, by not accepting help from others) tend to have dogs with higher levels of separation anxiety. This correlation suggests that behavioral problems in dogs could arise when owners interact with their dogs in an inappropriate way. The owners might not be providing social support when the dog needs it, or they might be absent or negligent when an inexperienced dog is exposed to a social threat. In contrast, a stable and balanced attachment relationship makes dogs feel safe, and it creates a strong emotional bond between dogs and their owners.

EMOTIONAL TIES

NOT LEAST because of this bond, dogs are often admired for their emotional sensitivity, and people living with dogs have always attributed emotions to their animal companions, assuming that dogs are happy, sad, angry and jealous just as humans are. Yet for years academic researchers refused to attribute emotions to animals. That attitude is changing slowly, and nowadays talking about emotions in dogs or other nonhuman species is no longer considered sacrilege.

Still an open question, though, is whether a dog's emotions signify what we think they do. Although some researchers accept that dog happiness and fear are akin to the human experience, experimental work has shown that dogs and humans differ in emotions of greater complexity, such as guilt. In humans, guilt arises when people violate a social rule, such as stealing someone's food.

Two independent studies, one led by cognitive scientist Alexandra Horowitz of Barnard College in 2009 and the other by canine behavioral researcher Julie Hecht, then at Eötvös Loránd, in 2012, examined dogs' behavior after they were told not to break just such a rule. In Horowitz's experiment, 14 dogs were told by their owners not to eat food on a table in the living room. The owners then left the room, presumably to give the dogs a chance to obey or disobey. But an experimenter then surreptitiously either offered the treat to the dogs (guaranteeing disobedience) or took it away (guaranteeing obedience).

Next the experimenter reported the dogs' behavior to the owners, sometimes truthfully, sometimes not, and directed the owners of "obedient" dogs to greet their pets in a friendly manner and to scold dogs they were told had disobeyed. All the dogs that were scolded, whether or not they actually ate the food, displayed in equal measure the behaviors that owners identified as signs of guilt, suggesting that dogs were reacting to the behavior of their owners—that is, scolding and a dissatisfied expression—rather than awareness of their own transgression. Hecht also noted that the dogs' demeanor was a survival mechanism of sorts, reporting that when asked about their habits at home, owners who observed guilty behavior said they were less likely to scold their dogs after discovering a misdeed.

No definitive research exists on dogs and sorrow, whether they feel their own or react to ours, but psychologists Deborah Custance and Jennifer Mayer, both then at Goldsmiths, University of London, were able to provide scientific evidence for the long-held belief that human crying evokes affiliated behavior in dogs. In a 2012 study, the experimenters observed the reaction of 18 dogs in a home setting as their owners and strangers hummed, talked or pretended to cry. Almost all the dogs approached the crying person, looked at her and touched her. These behaviors were much less fre-

Today people own dogs just for the pleasure of it, but in earlier times, dogs had to earn their keep by doing jobs such as helping with the hunt.

GETTY IMAGES (*herding dog, assistance dog and tapestry of hunt*); RICHARD LEVINE *Alamy (guide dog)*

© 2015 Scientific American

quent when the humans were talking or humming. Although owners may anthropomorphize the dogs' behavior and believe it to be a sign of empathetic skills, the authors of the study concluded that there is a simpler explanation. They argued that the human cry was similar to distress vocalizations of mammals, including dogs, so the cries evoked distress as opposed to empathy, which would have required the dog to recognize the humans' inner state.

Supporting this conclusion, a 2014 study led by psychologists Ted Ruffman and Min Hooi Yong of the University of Otago in New Zealand showed that listening to a human baby cry evokes stress in dogs, as revealed by an increase in the levels of cortisol in their blood. Needless to say, when your dog nuzzles you, his behavior is comforting whatever the impetus, but keep in mind that if you are tempted to elicit some affection by showing your sadness, your dog may not be feeling bad for you; he may just be feeling bad because he is stressed out.

DO AS I DO!

MUCH OF HUMAN CULTURE is based on social learning. Language, the rules of society and the use of objects are all transmitted from the old to the young and from peer to peer. Dogs are very keen to learn by observation, too. The ability to learn socially is widespread among animals, but learning from representatives of a different species is much rarer. Because dogs regard humans as their social companions, their eagerness to learn by observing our activities should not be surprising; shepherds have long known as much. Yet science began probing the depth of this canine facility only a few years ago.

One of the most common tests of observational abilities involves a simple detour task, in which a dog must go around a

ISTOCKPHOTO (cat)

BODY LANGUAGE

Decoding the Cat

Felines may be hard to study, but we have learned a few things about them

By Julia Calderone

Cats have a curious allure. Even the most pampered house cats seem to flaunt their independence, as if to say that they do not really need us to get by. Despite this hauteur—or perhaps because of it—many of us cannot resist bringing these regal creatures into our homes, litter boxes and all. In fact, cats outnumber canines as human companions, although we know surprisingly little about their cognition.

Our partnership with cats is long-standing. Feline DNA suggests that the domestic cat may have split from its wild counterpart in the Middle East nearly 10,000 years ago. In 2014 a study by Michael J. Montague of Washington University in St. Louis and his colleagues identified a set of genes that may have been crucial in the transformation of the prehistoric cat into the cuddly pets we know today. These genes have been linked to key behavioral traits, such as the ability to learn and reduced fearfulness, which would have helped cats adapt to life in human company.

Yet many mysteries remain in deciphering feline behavior and intelligence, particularly in contrast to our growing knowledge of dogs. This gap arose in part because of the more urgent need to study dogs. Negative interactions between humans and hostile or misbehaving dogs are common societal problems.

A bigger reason for our poor grasp of the feline mind stems from the challenges of cat behavior. Whereas the ancestors of dogs roamed in packs and learned sophisticated strategies for interacting socially with other animals, the wildcat progenitors of today's house cats were more solitary animals. The patterns that govern their exchanges with one another and humans are therefore harder to parse. Ádám Miklósi and his colleagues have found that like dogs, cats are able to follow a pointed finger to food, but if the setup is rigged (say, if the bowl is just out of reach), the cat will give up; a dog will creatively strategize or look to humans for help. "If there's a problem," says anthrozoologist John Bradshaw of the University of Bristol in England, a specialist in human-animal interaction, "cats try to solve it on their own. And if they fail, they just walk away."

Cats are also tough to manage in the laboratory. "The second you take a cat out of its own home, it becomes nervous," says Marieke Gartner, a psychologist at the University of Edinburgh. If the cat is in its own territory, Gartner continues, it will react more naturally. As a result, most studies of cats are based on observations in the home rather than controlled experiments in the lab.

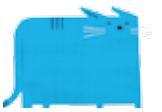
Given these challenges, we still have much to learn about cats. We can easily decipher a score of signals from dogs, but, Bradshaw says, "with cats, it's more like five or six." Some of the signs we know are listed to the right.

Julia Calderone is a freelance science writer based in New York City.

PURR The purr seems to serve multiple purposes: to share emotional states such as happiness or distress; to express urgency, typically when a cat wants to be fed; or to signal stress or injury.

MEOW Cats generally do not meow at one another, but they learn a repertoire of meows to communicate with humans. Typical meow meanings are specific to a given relationship: an owner knows what his or her cat's meow means but cannot necessarily understand that of another feline.

EARS Ears *back* signals aggression. Ears *forward* signals interest.



TAIL Tail *straight up* shows that the cat is fond of you but also acknowledges that you are slightly superior to it.

Tail *straight up and puffed out* means the cat is angry.

Tail *tucked between legs* means the cat is insecure, trying to get away or withdrawing from the world.

RUBBING ITS HEAD AND FACE ON THINGS A cat has glands on the corners of its lips, between its eye and ear, and under its chin; this behavior marks territory, and some scientists believe it could signal affection.

LYING ON ITS BACK, BELLY EXPOSED The cat is relaxed and trusts you.

KNEADING Kittens make this motion to stimulate their mother's milk. In adulthood, researchers suspect the behavior is affectionate and signals that the kneaded individual is in a superior, mothering role.

LICKING Cats of the same size and status groom one another frequently, which is thought to improve bonds and eliminate aggression within the colony. "It's a genuine demonstration of affection," Bradshaw says, "which in cat societies is very important."

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KENNAN HARVEY *Aurora Photos*

Search-and-rescue dogs are learning to form cooperative relationships not only with people but with machines; one day airborne robots might direct the dogs to the vicinity of a missing person.

fence of about three meters in length to reach a visible target (such as some food or a toy). In a 2001 study, animal behaviorist Péter Pongrácz and his team at Eötvös Loránd showed that family dogs need six or seven attempts to master this task through trial and error—but they can learn to make the detour after watching an expert dog complete the task only once. And the dogs learned equally well by watching a human expert.

The age-old imitation game that parents like to play with their babies is also helping researchers understand how dogs learn by observing. Mothers and fathers often demonstrate a specific action (such as touching the tip of the nose with their index finger) and then encourage their infant to do the same. In 2006 Topál, then at the Hungarian Academy of Sciences, and his team were the first to show that people could play a similar game with dogs. A human first trains the dogs to perform three or four tasks (such as turning around, jumping on a table or going around a cone) by demonstrating each of the actions and telling the dog, "Do it!" The dog receives a reward when it completes the task. Most dogs can learn these rules quickly. Then the human demonstrates new tasks (such as touching the cone with a hand). After regular practice, the dogs will naturally imitate such novel actions performed by their human companions.

The do-as-I-do game awakens the natural inclination of dogs to copy our behavior. Yet we do not always wish them to do so. Who wants a puppy to eat from the table, dig in the garden or "read" the newspaper? So humans often discourage dogs from imitating them, and the dogs quickly learn not to copy most activities performed by their human companions. Even so, the number of things dogs learn by watching us might surprise even people who have had dogs for years. Some dogs may learn to open doors by watching their owners turn the handle, or they may jump on a sled just because they see people having fun as they slide down a hillside. Indeed, the ability to learn from observation helps dogs master the rules necessary to fit in with human groups and their owners' idiosyncratic habits.

COOPERATION: GETTING PRACTICAL

IN MODERN WESTERN SOCIETY, dogs are often loved just because they are dogs. But dogs would probably not be around today if they had not proved themselves so useful to societies in the past—serving as household alarm systems, protecting the herd from wolves, pulling sledges. And that usefulness continues today as dogs assist the police (with drug detection, say) and help people living with disabilities. Guide dogs for the blind and dogs for people in wheelchairs or living with hearing impairment not only provide round-the-clock practical help but also fill important social roles, of which friendship is one of the most important.

Indeed, a vital element of dogs' social competence involves their impressive cooperative skills. In a useful partnership, each individual must display self-control, take notice of the other's goals and actions, and learn to take turns, so that at different times one or the other is in the lead. Studies have shown that guide dogs possess all these skills. In 2001 a detailed behavioral analysis of blind people and their guide dogs, conducted by animal behaviorist Szima Naderi, then at Eötvös Loránd, and her team revealed the fine-

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grained nature of the interaction as the two walk together, with each partner acknowledging the objectives of the other and switching leadership very rapidly. For example, the blind person initiates a turn to the left or right (because she knows where she wants to go) while the dog takes the lead in evading an obstacle in the street (because the canine can see it).

Dogs can also collaborate on tasks in which they seem to understand the consequences of coordinated action. In a study published in 2014, psychologists Ljerka Ostojic and Nicola Clayton, both at the University of Cambridge, reported on dogs' ability to solve the so-called loose-string task, considered a benchmark test for joint problem solving. In the usual setup, the partners are given a box from which two strings emerge. In fact, they are seeing two ends of a single string. If both partners take an end and pull simultaneously, they will move the target object (placed at the back of the box) to within their reach. If only one tugs at the string, however, it will slip out of the apparatus without moving the prize. During the experiment, dogs learned to get the prize by coordinating their behavior with either a human or a dog partner. Thus, dogs were able to recognize that the specific actions of the other were necessary for their own success. And this rapid development of cooperative behavior between the dogs and their partners explains why dogs are so good at helping humans in tasks that are narrowly defined, such as leading a sightless person through busy city streets. [For more on how animals work together to solve problems and learn skills, see "The Social Genius of Animals," by Katherine Harmon Courage, on page 106.]

DOGS IN THE HIGH-TECH FUTURE

THE INVASION of modern technology into everyday life may have dog owners wondering how their relationship with their companions will fare in the digital age. Yet dogs have already begun to interact with today's technology and even to form ad hoc partnerships with devices. In a recent experiment published in *PLOS ONE,* animal behaviorist Anna Gergely, then at Eötvös Loránd, and her team delivered some food to family dogs via a remote-controlled car. After a few such interactions, the dogs began to look at, touch or push the car when it was not moving, as if their goal was to get the car to do its "job." On the surface, the dogs' actions resembled those they displayed toward their owners in similar circumstances. In principle, if the abilities of devices grow more complex, so should the relationship between dogs and machines.

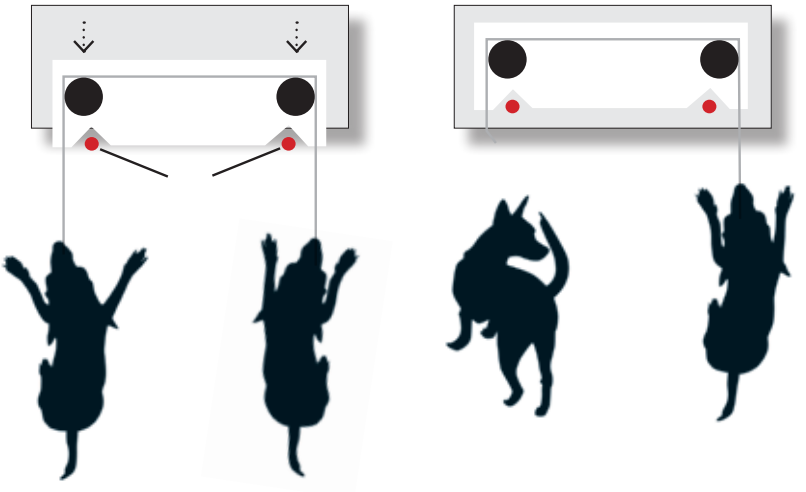
Such dog-machine interactions can also have practical benefits. In a recent project headed by computer engineering professor Bernhard Plattner of the Swiss Federal Institute of Technology in Zurich and supported by the Swiss National Science Foundation, researchers tested the idea that searches for people lost in the woods or mountains would be more effective if the human rescuers were complemented by a team of dogs and airborne robots armed with cameras. Animal behaviorist Linda Gerencsér of Eötvös Loránd worked with dog trainer Barbara Kerekes to teach four dogs to follow a flying robot over a distance of 100 to 150 meters. They also trained the dogs to stop following the robot and start searching for the missing person by smell if they saw the robot hovering above a specific location. Dogs would then alert the human rescuers by barking if they found the missing person. Researchers believe that as the technology develops, such machine-aided groups will outperform traditional rescue teams, especially if dogs acknowledge the flying robot as a social partner—one to which they might respond with the eagerness they would show to a human companion.

Human life is growing ever more distant from the natural world, and dogs will never be able to understand the breadth of these changes. But their social competence will help them successfully negotiate an evolving society, just as they have since beginning their long journey alongside the human family. SA

Ádám Miklósi is a biologist and head of the department of ethology at Eötvös Loránd University in Budapest. He is a leading scientist in the study of human-dog interactions, with special interest in cognitive abilities of dogs.

CANINE TEAMWORK

In the loose-string task, two dogs learn that if they pull together, they can move a treat (*red*) within reach. But if one pulls and the other does not, the string slips out and the prize is lost.



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Dolphins are commonly used in animal-assisted therapies.

CAN ANIMALS AID THERAPY?

Is animal-assisted therapy the cat's meow or a red herring?

By Scott O. Lilienfeld and Hal Arkowitz

In 1857 British novelist George Eliot wrote, "Animals are such agreeable friends. They ask no questions and they pass no criticism." So it is no surprise that scholars have long been intrigued by the possibility that animals possess largely untapped therapeutic powers. But are animals good for our psychological and physical health, either as pets or as "therapists"?

Most Americans are animal lovers; about 65 percent of U.S. households contain one or more pets, according to the American Pet Products Association. Several, but not all, studies suggest that those of us who own pets tend to be somewhat happier than those of us who do not. In addition, research by Erika Friedmann and her colleagues at the University of Maryland School of Nursing shows that pet ownership predicts one-year survival rates among victims of heart attacks.

Though interesting and potentially important, studies such as these are difficult to interpret because pet owners may differ in unmeasured ways from people who do not own pets. For example, pet owners may be better adjusted psychologically and have fewer cardiac risk factors (they may eat healthier diets and experience lower levels of hostility) than non–pet owners.

EASING STRESS?

To unravel the potential influences of pets on well-being, researchers must conduct experiments that randomly assign some people, but not others, to receive a pet, either in the laboratory or in their home. Studies by psychologists Karen Allen, then at the University at Buffalo, and James Blascovich of the University of California, Santa Barbara, and their colleagues demonstrate that the presence of a favorite pet during a stressful task—such as performing difficult mental arithmetic—largely prevents spikes in participants' blood pressure. In contrast, the presence of a friend does not. In addition, Allen's work shows that stressed-out, hypertensive stockbrokers who were randomly assigned to adopt either a pet dog or cat ended up with lower blood pressure than those who were not. These studies suggest that the presence of pets may lower our blood pressure and stress levels, although they do not tell us the reasons for this effect. They also do not inform us whether we would observe similar effects with other preferred stimuli, such as a good luck charm or a favorite doll.

Few would contest the claim that pets can give us comfort, especially in times of strain or loneliness. A far more controversial question concerns the effectiveness of animal-assisted therapy (AAT), defined as the use of an animal as either a

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treatment by itself or an addition to an existing treatment, such as psychotherapy. The animals used in various forms of AAT are a veritable menagerie: horses, dogs, cats, rabbits, birds, fish, guinea pigs and, perhaps best known of all, dolphins. In turn, the psychological problems for which AATs are used include schizophrenia, clinical depression, anxiety disorders, eating disorders, attention-deficit/hyperactivity disorder, autism and a host of developmental disabilities.

Popularized largely by Yeshiva University psychologist Boris Levinson in the 1960s, AATs appear to be surprisingly common: a 1973 survey by Oklahoma State University psychologist Susan S. Rice and her colleagues revealed that 21 percent of therapists in the psychotherapy division of the American Psychological Association incorporated animals into their treatment in some fashion. Whether this percentage has changed in 42 years is unknown.

LEISURE VS. THERAPY

DO AATS WORK? To make some inroads into this question, we need to distinguish between two different uses of animals: recreation and psychotherapy. Some uses of animals are purely recreational: their goal is to allow their human companions to have fun. There is scant dispute that interacting with friendly animals can "work" for such purposes because such activities often make people feel happier temporarily. To show that AATs work, however, researchers must demonstrate that animals produce enduring effects on people's psychological health, not merely short-term changes in mood, such as pleasure, relaxation or excitement.

Probably the most extensively researched AAT is dolphin-assisted therapy (DAT), which is most commonly used for children with autism or other developmental disabilities. DAT is practiced not only in the U.S.—primarily in Florida and Hawaii—but also in Mexico, Israel, Russia, Japan, China and the Bahamas, among other countries. Typically during DAT sessions children interact with a captive dolphin in the water while performing rudimentary manual tasks, such as placing rings on a peg. In many cases, the dolphin presumably serves as a "reinforcer" for appropriate child behaviors. DAT Web sites advance strong claims regarding this treatment's effectiveness; one in Turkey asserts that "this field of medicine has shown extraordinary results of the therapy and breakthroughs in outcomes" as compared with conventional treatments, including medication and therapy (see www.antalyadolphinarium.com). Do the data support these assertions?

WEB SITES ADVANCE STRONG CLAIMS REGARDING EFFECTIVENESS. DO THE DATA SUPPORT THESE ASSERTIONS?

Psychologist Lori Marino, then at Emory University, and one of us (Lilienfeld) examined the research findings regarding DAT in two reviews, one published in 1998 and the second in 2007. We found the evidence lacking for DAT's effectiveness. In many cases, researchers had shown only that children who received DAT displayed improvements on some psychological measures as compared with children who did not. Yet such results do not exclude the possibility that these changes would have occurred with the mere passage of time. In still other cases, researchers did not rule out the possibility that reported improvements were merely short-term mood effects rather than lasting changes in symptoms. Finally, no researcher adequately excluded the possibility that the observed effects could have been produced by any animal or, for that matter, by any highly pleasurable stimulus. The research literature for other AATs appears to be no more definitive.

HIDDEN COSTS

WHY SHOULD WE CARE about whether AATs work? After all, if children seem to enjoy them and parents are willing to pay for them, why worry? There are at least three reasons. First, AATs can produce what economists term "opportunity costs"—the time, money and effort expended in seeking out ineffective treatments. Because of such costs, parents and children may forfeit the chance to seek out effective treatments. In the case of DAT, opportunity costs are far from trivial because treatments frequently cost $3,000 to $5,000, not including the price of travel and lodging. Second, at least some AATs may be physically hazardous. For example, in DAT it is not legally required that dolphins be screened for infectious diseases. Moreover, there have been multiple reports of children injured by dolphins in DAT sessions. Third, some AATs result in largely unappreciated costs to the animals themselves. For example, removing dolphins from the wild for transfer to DAT facilities not only separates them from their families but also often results in the death of many dolphins within each pod.

So, to the bottom line: Are animals good for our psychological and physical health? Undoubtedly, many animals can be valued companions and provide social support; they can also make us feel better in the short term. It is possible that pets can be of particular help to people with depression or to children who have been severely neglected—for whom loneliness and lack of social support are often common problems. Still, further research will be needed to investigate this possibility. Moreover, whether animals—including dolphins—produce long-term changes in the core symptoms of other psychological conditions, such as autism, developmental disabilities or anxiety disorders, is another matter altogether. To this question, we must reserve the verdict sometimes delivered in Scottish courts: "unproven." SA

Scott O. Lilienfeld and **Hal Arkowitz** serve on the board of advisers for *Scientific American Mind*. Lilienfeld is a psychology professor at Emory University, and Arkowitz is a psychology professor at the University of Arizona. The authors thank Lori Marino for her generous help with this article.

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The Dog's Universe

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Illustration by Bomboland

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THE SCIENCE OF DOGS AND CATS

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FROM WOLF

Scientists are racing to solve the enduring mystery of how a large, dangerous carnivore evolved into a playful companion *By Virginia Morell*

Photographs by Peter Rigaud

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WHEN YOU HAVE CARED FOR DOGS AND WILD WOLVES FROM THE TIME THEY are little more than a week old and have bottle-fed and nurtured them day and night, you are wise to their differences. Since 2008 Zsófia Virányi, an ethologist at the Wolf Science Center in Austria, and her colleagues have been raising the two species to figure out what makes a dog a dog—and a wolf a wolf. At the center, the researchers oversee and study four packs of wolves and four packs of dogs, containing anywhere from two to six animals each. They have trained the wolves and dogs to follow basic commands, to walk on leashes and to use their nose to tap the screen of a computer monitor so they can take cognition tests. Yet despite having lived and worked with the scientists for seven years, the wolves retain an independence of mind and behavior that is most undoglike.

"You can leave a piece of meat on a table and tell one of our dogs, 'No!' and he will not take it," Virányi says. "But the wolves ignore you. They'll look you in the eye and grab the meat"—a disconcerting assertiveness that she has experienced on more than one occasion. And when this happens, she wonders yet again how the wolf ever became the domesticated dog.

"You can't have an animal—a large carnivore—living with you and behaving like that," she says. "You want an animal that's like a dog; one that accepts 'No!'"

Dogs' understanding of the absolute no may be connected to the structure of their packs, which are not egalitarian like those of the wolves but dictatorial, the center's researchers have discovered. Wolves can eat together, Virányi notes. Even if a dominant wolf flashes its teeth and growls at a subordinate, the lower-ranked member does not move away. The same is not true in dog packs, however. "Subordinate dogs will rarely eat at the same time as the dominant one," she observes. "They don't even try." Their studies also suggest that rather than expecting to cooperate on tasks with humans, dogs simply want to be told what to do.

How the independent-minded, egalitarian wolf changed into the obedient, waiting-for-orders dog and what role ancient humans played in achieving this feat baffle Virányi: "I try to imagine how they did it, and I really can't."

Virányi is not alone in her bafflement. Although researchers have successfully determined the time, location and ancestry of nearly every other domesticated species, from sheep to cattle to chickens to guinea pigs, they continue to debate these questions for our best friend, *Canis familiaris*. Scientists also know why humans developed these other domesticated animals—to have food close at hand—but they do not know what inspired us to allow a large, wild carnivore into the family homestead. Yet dogs were the first domesticated species, a status that makes the mystery of their origin that much more perplexing.

As inscrutable as the mystery is, scientists are piecing it together. In the past few years they have made several breakthroughs. They can now say with confidence that contrary to received wisdom, dogs are not descended from the gray wolf species that persists today across much of the Northern Hemisphere, from Alaska to Siberia to Saudi Arabia, but from an unknown and extinct wolf. They are also certain that this domestication event took place while humans were still hunter-gatherers and not after they became agriculturalists, as some investigators had proposed.

At what time and in what location wolves became dogs and whether it was only a one-time event are questions that a large research team, composed of once competing scientists, has just started to tackle. The researchers are visiting museums, universities and other institutions around the world to study collections of canine fossils and bones, and they are readying genetic samples from ancient and modern dogs and wolves for the most comprehensive comparison to date. When they are finished, they will be very close to knowing when and where—if not exactly how—wolves first began down the path toward becoming our trusted companions. Answers to these questions will complement the growing body of evidence for how humans and dogs influenced one another after that relationship was first forged.

MIXED SIGNALS

WHEN MODERN HUMANS arrived in Europe perhaps 45,000 years ago, they encountered the gray wolf and other types of wolves, including the megafaunal wolf,

IN BRIEF

The dog was the first domesticated species. Yet despite years of research, scientists have struggled to figure out when, where and how it originated. **Recent DNA studies** have thrown new light on the dog's wolf ancestor, and an ambitious project is now under way to nail down the timing and location of dog domestication. **Such insights** will complement clues to how the human-dog relationship shifted in the millennia that followed.

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which pursued large game such as mammoths. By that time wolves had already proved themselves among the most successful and adaptable species in the canid family, having spread across Eurasia to Japan and into the Middle East and North America. They were not confined to a single habitat type but flourished in tundra, steppelands, deserts, forests, coastal regions and the high altitude of the Tibetan Plateau. And they competed with the newly arrived humans for the same prey—mammoths, deer, aurochs, woolly rhinoceroses, antelopes and horses. In spite of this competition, one type of wolf, perhaps a descendant of a megafaunal wolf, apparently began living close by to people. For many years scientists concurred on the basis of small portions of the genome that this species was the modern gray wolf (*Canis lupus*) and that this canid alone gave rise to dogs.

But last January geneticists discovered that this long-held "fact" was wrong. Repeated interbreeding between gray wolves and dogs, which share 99.9 percent of their DNA, had produced misleading signals in the earlier studies. Such consorting between the two species continues today: wolves with black coats received the gene for that color from a dog; shepherd dogs in Georgia's Caucasus Mountains mate so often with the local wolves that hybrid ancestors are found in both species' populations, and between 2 and 3 percent of the sampled animals are first-generation hybrids. (Building on the admixture theme, in June researchers writing in *Current Biology* reported about the sequencing of DNA from a 35,000-year-old wolf fossil from Siberia. This species appears to have contributed DNA to high-latitude dogs such as huskies through ancient interbreeding.)

Analyzing whole genomes of living dogs and wolves, last January's study revealed that today's Fidos are *not* the descendants of modern gray wolves. Instead the two species are sister taxa, descended from an unknown ancestor that has since gone extinct. "It was such a long-standing view that the gray wolf we know today was around for hundreds of thousands of years and that dogs derived from them," says Robert Wayne, an evolutionary geneticist at the University of California, Los Angeles. "We're very surprised that they're not." Wayne led the first genetic studies proposing the ancestor-descendant relationship between the two species and more recently was one of the 30 co-authors of the latest study, published in *PLOS Genetics,* that debunked that notion.

More surprises may come from renewed efforts to nail down the timing and location of dog domestication. Previous studies left a confusing trail. The first analysis, carried out in 1997, focused on the genetic differences between dogs and gray wolves and concluded that dogs may have been domesticated some 135,000 years ago. A later study by some members of the same group indicated that dogs originated in the Middle East. But another analysis, which examined the DNA of 1,500 modern dogs and was published in 2009, argued that dogs were first domesticated in southern China less than 16,300 years ago. Then, in 2013, a team of scientists compared the mitochondrial genomes of ancient European and American dogs and wolves with their modern counterparts. It concluded that dogs originated in Europe between 32,000 and 19,000 years ago.

A dog at the Wolf Science Center outside Vienna, Austria, awaits permission to eat. Wolves, even those raised by people, lack such respect for human authority.

Evolutionary biologist Greger Larson of the University of Oxford, who is co-leading the recently launched multidisciplinary dog-domestication project, says the previous studies, while important, have shortcomings. He faults the 1997 and 2009 studies for relying solely on DNA from modern dogs and the last one for its geographically limited samples. "You can't solve this problem by using modern animals alone as windows to the past," Larson says. The studies of modern dog DNA are not sufficiently informative, he explains, because people have moved and interbred dogs around the world numerous times, blurring their genetic heritage. Any regional signatures that might have helped identify where they were domesticated have long since been lost.

To further muddy the picture, "wolves have a ridiculously broad distribution across the world," Larson explains. In contrast, he points out, the ancestors of most other domesticated species, such as sheep and chickens, had much smaller geographical ranges, making it far easier to trace their origins.

Larson suspects that several geographically disparate populations of the ancestral wolf species may have contributed to the making of today's dog. It would not be the first time that such a thing happened: Larson has shown that pigs were domesticated twice—once in the Near East and once in Europe. Intriguingly, enigmatic fossils from Belgium, the Czech Republic and southwestern Siberia that date to between 36,000 and 33,000 years ago and exhibit a mix of wolf and dog features hint at the possibility of at least three independent instances of domestication attempts from an ancestral wolf. But the anatomical characteristics of these fossils alone cannot answer the question of where dogs came from.

To solve the dog-domestication puzzle, Larson and his collaborators are using two key techniques employed in the pig study: they are undertaking a more thorough analysis of thousands of modern and ancient samples of dog and wolf DNA from individuals across the globe

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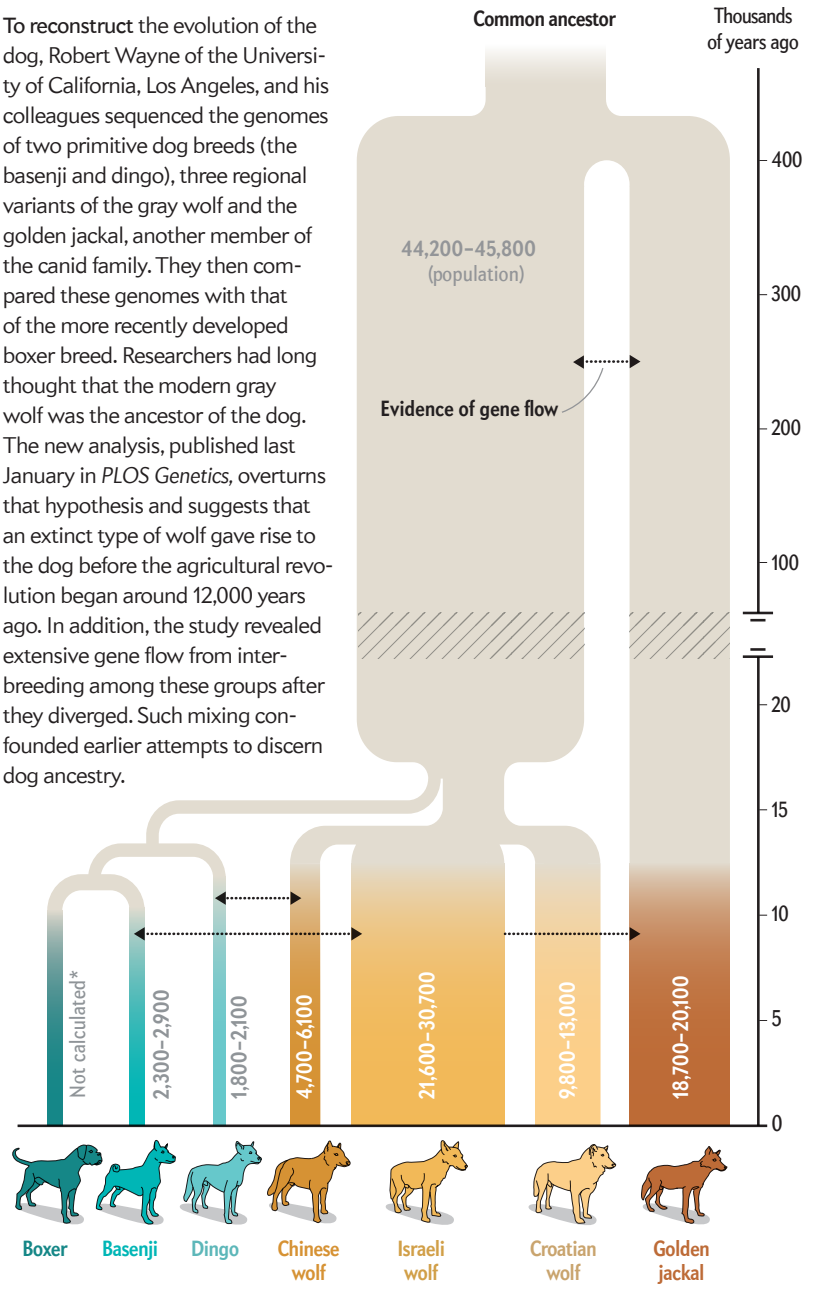
and are using a fairly new technique for measuring bones. Called geometric morphometrics, this method enables scientists to quantify certain traits, such as the curves of a skull, and so better compare the bones of individuals.

Previously researchers relied primarily on the length of a canid's snout and the size of the canine teeth to distinguish dogs from wolves. Dogs' snouts are generally shorter, their canines are smaller, and their teeth are on the whole more crowded than those of wolves. The new method should identify other, perhaps more telling differences. Together these techniques should yield a far more detailed picture of dog domestication than any other approach has to date.

FINDINGS

A Complex History

To reconstruct the evolution of the dog, Robert Wayne of the University of California, Los Angeles, and his colleagues sequenced the genomes of two primitive dog breeds (the basenji and dingo), three regional variants of the gray wolf and the golden jackal, another member of the canid family. They then compared these genomes with that of the more recently developed boxer breed. Researchers had long thought that the modern gray wolf was the ancestor of the dog. The new analysis, published last January in *PLOS Genetics*, overturns that hypothesis and suggests that an extinct type of wolf gave rise to the dog before the agricultural revolution began around 12,000 years ago. In addition, the study revealed extensive gene flow from interbreeding among these groups after they diverged. Such mixing confounded earlier attempts to discern dog ancestry.



*Boxer population size could not be estimated based on the available data.

CLOSE ENCOUNTERS

ALTHOUGH THE WHEN and where of dog domestication remain open questions, scientists now have a general idea of which kind of human society was the first to establish a close relationship with dogs. Perhaps not surprisingly, this question, too, has generated debate over the years. Some investigators have argued that settled agriculturalists had that distinction. After all, the other domesticated animal species all entered the human realm after people started farming and putting down roots. But other researchers credited earlier hunter-gatherers with being the first to have dogs. Wayne says that his team's latest DNA study has at last ended this part of the debate. "The domestication of the dog occurred prior to the agricultural revolution," he asserts. "It happened when people were still hunter-gatherers," sometime between 32,000 and 18,800 years ago. (Agriculture is thought to have begun in a big way roughly 12,000 years ago in the Middle East.)

And that finding leads back to the questions Virányi and most everyone who owns and loves a dog has: How did these hunter-gatherers do it? Or did they? What if the first dogs—which, it is important to remember, would have at first been more wolf than dog—showed up on their own?

The genus *Canis* goes back about seven million years, and although some members of that group, such as jackals and the Ethiopian wolf, lived in Africa, the birthplace of humanity, there is no evidence that the earliest humans tried to domesticate any of these species. Only after modern humans spread out from Africa and into Europe 45,000 years ago did the wolf-dog-human triad begin to form.

Hints about the evolving relationship between canids and early modern humans have come from the paleontological and archaeological records. Take the canid remains unearthed between 1894 and 1930 at Předmostí, a roughly 27,000-year-old settlement in the Bečva Valley in what is now the Czech Republic. The ancient people who lived and died there are known to us as the Gravettians, after a site with similar cultural artifacts in La Gravette, France. The Czech Gravettians were mammoth hunters, killing more than 1,000 of

SOURCE: "GENOME SEQUENCING HIGHLIGHTS THE DYNAMIC EARLY HISTORY OF DOGS." BY ADAM H. FREEDMAN ET AL., IN *PLOS GENETICS*, VOL. 10, NO. 1, ARTICLE NO. e1004016; JANUARY 16, 2014

Graphic by Tiffany Farrant-Gonzalez, Illustration by Portia Sloan Rollings (dogs)

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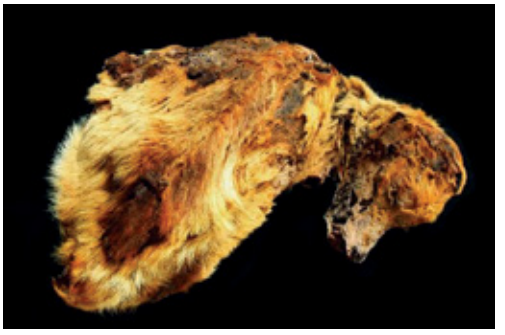
the great creatures at this one site alone. They ate the behemoths' meat, used their shoulder blades to cover human remains and decorated their tusks with engravings. They also killed wolves. Canids are the most abundant type of mammal at the site after mammoths, and their remains include seven complete skulls.

But some of the canid skulls do not look exactly like those of wolves. Three in particular stand out, says Mietje Germonpré, a paleontologist at the Royal Belgian Institute of Natural Sciences in Brussels. Compared with the wolf skulls found at Předmostí, the three unusual ones "have shorter snouts, broader braincases and crowded teeth," she notes.

These kinds of anatomical changes are the first signs of domestication, Germonpré and others say. Similar changes are found in the skulls of the silver foxes that are the focus of a famous, long-running experiment at Novosibirsk State University in Russia. Since 1959 researchers there have selected the foxes for tameness and bred them. Over the generations their coats have become spotted, their ears floppy, their tails curly, their snouts shorter and wider—even though the scientists have been selecting only for behavior. Similar changes are seen in other domesticated species, including rats and mink. Investigators have yet to explain why docile animals are consistently altered in these ways. They do know that the tame silver foxes have smaller adrenal glands and much lower levels of adrenaline than their wild counterparts.

Last year other scientists came up with a testable hypothesis: tame animals may have fewer or defective neural crest cells. These embryonic cells play a key role in the development of the teeth, jaws, ears and pigment-producing cells—as well as the nervous system, including the fight-or-flight response. If they are right, then all those cute domestic traits—spotted coats, curly tails, floppy ears—are a side effect of domestication.

Germonpré believes that the apparent domestication at Předmostí was a dead-end event; she doubts that these animals are related to today's dogs. Nevertheless, to Germonpré, "they are dogs—Paleolithic dogs." She says these early dogs probably looked very much like today's huskies, although they would have been larger, about the size of a German shepherd. Germonpré calls the Předmostí specimens "dogs" because of what she interprets as some type of relationship between the canids and the Gravettians. For instance, a dog's lower jaw was found near a child's skeleton, according to the diary of the original excavator.



Dogs from the roughly 27,000-year-old site of Předmostí, Czech Republic, were seemingly bred for sacrifice (*skull, top*); dogs bred by the Chiribaya in Peru 1,000 years ago were revered herders (*mummy, bottom*).

The dogs were also included in rituals in ways that other species were not. In one case, a Gravettian tucked what is most likely a piece of mammoth bone between the front teeth of one of the dog skulls after the animal died and arranged its jaws so that they clamped together on the bone. Germonpré suspects that an ancient mammoth hunter placed the bone there as part of a ritual related to hunting, or to help sustain in death an animal the hunter revered, or to enable the dog to assist a human in the afterlife. "You see this kind of thing in the ethnographic record," she says, citing, as one example, a Chukchi ceremony in Siberia for a deceased woman in the early 20th century. A reindeer was sacrificed and its stomach placed in the mouth of a dead dog's head, which was then positioned to protect the woman on her death journey.

Many researchers imagine that these early people set about making the wolf into the dog to help us hunt big game. In her book *The Invaders,* published by Harvard University Press earlier this year, anthropologist Pat Shipman argues that the first dogs (or wolf-dogs, as she calls them) were like a new and superior technology and helped the mammoth-hunting modern humans outcompete the Neandertals. But she, Wayne, Larson and others think that wolves joined forces with humans on their own; that the canny, adaptable canids identified us as a new ecological niche they could exploit. The alternative scenario—people brazenly raiding wolf dens to steal pups young enough for taming—would have been a dangerous undertaking. And raising wolves in camps with young children would have presented another serious risk.

"We didn't do [domestication] deliberately—not at first," Larson surmises. Instead wolves most likely started following people for the same reason that ants trail into our kitchens—"to take advantage of a nutritional resource, our trash." Over time some of these camp-following wolves increasingly lost their fear of people—and vice versa—and a mutually beneficial relationship developed. Wolf-dogs would sniff out prey for us, and we would share the resulting meat with them. (Circumstantial evidence for this scenario comes from the silver fox experiment. By selecting foxes that were less fearful of humans, the researchers at Novosibirsk eventually developed a silver fox that runs to greet people. Most silver foxes in captivity hide in the back of their cage.)

There is just one problem with this imagined event, at least at Předmostí: Germonpré's early dogs were not eating mammoth meat even though that is what the humans were dining on; isotopic analysis of the Paleolithic dogs' bones indicates that they were eating reindeer, which was not a favored food of the people who inhabited the site. The Předmostí dogs also had broken teeth and severe facial injuries, many of which had healed. "Those could be signs of fighting with other dogs," Germonpré says, "or of being hit

MIETJE GERMONPRÉ Royal Belgian Institute of Natural Sciences (*skull*); MARIANA BAZO Reuters (*mummy*)

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Wild at heart: Exactly how the dog's wolf ancestor first began down the path to becoming our trusted companion may remain a mystery.

with sticks." She pictures the human-dog bond developing via the mammoth hunters' canid rituals. In this scenario, the hunter-gatherers brought pups to their camps, perhaps after killing the adult wolves, just as many modern nomadic peoples bring baby or young animals to their settlements. The mammoth bones at Předmostí show no signs of being gnawed by canids, which suggests they were not free to roam and scavenge people's scraps. Rather humans probably tied the canids up, fed them what appears to have been second-rate food, given that the humans were not eating it, and even bred them—all to ensure a ready supply of victims for their ritualistic sacrifices.

Breeding wolves in captivity would lead to the anatomical changes that Germonpré has documented in the Předmostí dogs and could even produce a less fearful and independent animal as seen in the Novosibirsk silver foxes.

Confined, beaten, fed a restricted diet, the dogs at Předmostí would likely have understood the meaning of "No!" There is no evidence at Předmostí or other comparably old sites where dog remains have been uncovered that the ancient hunter-gatherers there regarded the canines as their friends, companions or hunting pals, Germonpré observes: "That relationship came later."

SHIFTING FORTUNES

IF GERMONPRÉ IS RIGHT, then dog domestication may have begun quite early and under circumstances that were not favorable for the dogs. Not every scientist agrees that Germonpré's dogs are dogs, however. Some prefer the wolf-dog designation or simply "wolf" because their taxonomic status is not clear either from their morphology or from their genetics. (Larson expects to resolve this question over the course of his mega project.)

The earliest undisputed dog on record, a 14,000-year-old specimen from a site called Bonn-Oberkassel in Germany, tells a very different story of dog domestication, evincing a much more affectionate bond between humans and canines. In the early 1900s archaeologists excavating the site found the dog's skeleton interred in a grave with the remains of a man about 50 years old and a woman about 20 to 25. When researchers see such associations, they know they are looking at a fully domesticated animal—one that is treasured and regarded so highly that it is given a burial as if it, too, were a member of its human family.

The Bonn-Oberkassel dog is not the only ancient hound to have received such honors. In Israel, at Ain Mallaha, a hunter-gatherer site dating to 12,000 years ago in the upper Jordan Valley, archaeologists discovered what is perhaps the most famous dog-human burial. The skeleton of an elderly person lies curled on its right side, its left arm stretched out under the head, with the hand resting gently on a puppy. The dog was about four to five months old and was placed there, archaeologists think, to be a companion to the deceased. Unlike the Předmostí dogs, this puppy was not battered; its remains were arranged lovingly with someone who may have cared for it.

Although such touching dog-human scenes are rare during this period, dog burials are not. And after about 10,000 years ago, the practice of entombing dogs increased. No other animal species is so consistently included in human mortuary rituals. People had come to see dogs in a different light, and this shift in attitude

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had a profound effect on dogs' evolution. Perhaps during this period dogs acquired their human social skills, such as abilities to read our facial expressions, understand our pointing gestures and gaze into our eyes (which increases oxytocin—the love hormone—in both dog and owner).

"Dog burials happen after hunting moves away from the open plains and into dense forests," says Angela Perri, a zooarchaeologist at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, and a specialist on these burials. "Dogs in open environments might be good for helping you transport meat from killed mammoths but wouldn't necessarily help you hunt them," she says, noting that elephant hunters do not use dogs. "But dogs are excellent for hunting smaller game, such as deer and boar," that live in forests.

Beginning at least 15,000 years ago and probably somewhat earlier, Perri says, hunter-gatherers in Europe, Asia and the Americas began depending on their dogs' hunting skills for survival. Researchers cannot trace a direct genetic line from those animals to our pet pooches; nevertheless, they say, these animals were unquestionably dogs. "Good hunting dogs can find fresh tracks, and guide the hunters to the prey, and hold them at bay," says Perri, who has joined traditional hunters and their dogs in Japan and the U.S. "When people start using dogs for hunting, you see a switch in how people view them, and you start finding dog burials across the world." Such burials are not rituals or sacrifices, she emphasizes: "These are burials of admiration, where the dogs are interred with ocher, stone points and blades—male tools of hunting."

One of the most elaborate dog burials comes from Skateholm, Sweden, and is dated to about 7,000 years ago. Several dogs were found interred in the same area with dozens of humans. One was particularly celebrated and given the finest treatment there of anyone, human or dog. "The dog was laid on its side, flint chips were scattered at its waist, and red deer antlers and a carved stone hammer were placed with it, and it was sprinkled with red ocher," Perri says. There is no indication of why this dog was so revered, but she suspects that it must have been an excellent hunter and that its human owner mourned its death. "You see this relationship among hunters and their dogs today and in the ethnographic record," Perri observes, noting that Tasmanian hunter-gatherers in the late 19th century were quoted as saying, "Our dogs are more important than our children. Without them, we couldn't hunt; we wouldn't survive."

Early dogs provided other important services, too. The first known attempt at the kind of intentional selection that has shaped the evolution of *C. familiaris* comes from a site in Denmark dating to 8,000 years ago. The ancient hunter-gatherers there had three sizes of dogs, possibly bred for certain tasks. "I didn't expect to see something like dog breeds," Perri says, "but they had small, medium and large dogs." It is not clear what they used the small dogs for, but the medium-sized animals had the build of hunting dogs, and the larger ones, which were the size of Greenland sled dogs (about 70 pounds), most likely transported and hauled goods. With their warning barks, all the dogs would have served as camp sentinels, too.

The dog's status plunged when people developed farming. In early agricultural settlements, dog burials are rare. "The difference is so strong," Perri says. "When people are living as hunter-gatherers, there are tons of dog burials." But as agriculture spreads, the burials end. "Dogs are no longer as useful." That fall from grace, though, did not doom them to extinction—far from it. In many places, they began to turn up on the dinner table, providing a new reason to keep dogs around.

Not all agricultural cultures consigned Fido to the menu, however. Among those groups that tended livestock, dogs were sometimes bred for herding. Those that proved their worth could still end up pampered in the afterlife. In 2006 archaeologists discovered 80 mummified dogs buried in graves next to their human owners at a 1,000-year-old cemetery near Lima, Peru. The dogs had protected the Chiribaya people's llamas and, in return for their service, were well treated in life and death. Nearly 30 of the dogs were wrapped in finely woven llama-wool blankets, and llama and fish bones were set close to their mouth. The region's arid climate mummified the dogs' remains, preserving their fur and tissue. Unwrapped, the mummies resemble the small street dogs that roam Lima today, looking for a human to take them in and tell them what—and what not—to do. (That resemblance notwithstanding, the Chiribaya herding dogs are not related to Lima's modern-day mutts. Nor is there any evidence to support claims linking any of the breeds of antiquity anywhere to the modern, standard breeds of the American Kennel Club.)

Although the Chiribaya dogs and other dog burials in the Americas hail from the wrong place and time to represent the earliest stages of domestication, Larson and his colleagues are happily measuring their bones and sampling their DNA. That is because these early North American dogs descended from ancient European or Asian dogs; their bones and genes will help the scientists determine how many dog-domestication events occurred and where they took place. Thus far in their attempt to study as many ancient canids as possible, the researchers have analyzed upward of 3,000 wolves, dogs and other specimens that do not readily fall into either box. More than 50 scientists worldwide are helping with the effort. They expect to have a paper ready on their initial findings this year.

Will we then finally know where and when the dog became domesticated? "I expect we'll be very close to an answer," Larson says. But we still won't know exactly how some long-lost type of wolf managed to become a creature that respects "No." SA

Virginia Morell is a science writer based in Oregon. She covers evolution and animal behavior for *Science* and *National Geographic*, among other publications. Her latest book is *Animal Wise* (Crown, 2013).

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Inside the Dog Mind

New science reveals the multiple intelligences of our best friend

By Gareth Cook

JUST ABOUT EVERY DOG OWNER IS convinced that their dog is a genius. For a long time scientists did not take such pronouncements very seriously, but research now suggests that canines are indeed quite bright and, in some ways, unique. Brian Hare, associate professor in the department of evolutionary anthropology and the Center for Cognitive Neuroscience at Duke University, is one of the leading figures in the quest to understand what dogs know. Founder of the Duke Canine Cognition Center, Hare has written a book, *The Genius of Dogs,* with his wife, journalist Vanessa Woods.

Your dog might be a lot smarter than you realize.

COOK: What is the biggest misconception people have about the dog mind?
HARE: That there are "smart" dogs and "dumb" dogs. There's still this throwback to a unidimensional version of intelligence, as though there is only one type of intelligence that you either have more or less of.

In reality, there are various types of intelligence. Different dogs are good at different things. Unfortunately, the clever strategies some dogs are using are not apparent without playing a cognitive game. This means people can often underestimate the intelligence of their best friend. The pug drooling on your shoe may not look like the brightest bulb, but she comes from a long line of successful dogs and is a member of perhaps the most successful mammal species on the planet besides us. Rest assured: she is a genius.

COOK: What are the "different things" that dogs are good at? What are the areas of dog intelligence you have studied?
HARE: We know that, as a species, dogs are remarkable in certain areas, such as taking someone else's visual perspective or learning from someone else's actions. In particular, I've been interested in how dogs recruit help. Still, most of my research with dogs has been about the cooperative way they use human communicative gestures. Or put more simply, how they can interpret our gestures to understand us or get what they want.

COOK: But other animals are intelligent, right? What makes dogs unique?
HARE: Absolutely. Other animals have their own unique genius that was shaped by nature. In the case of dogs, it happens to be their ability to read our communicative gestures. We take it for granted that dogs can effortlessly use our pointing gestures to find a hidden toy or morsel of

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food, but no other species can spontaneously read our communicative gestures as flexibly as dogs can. It allows them to be incredible social partners with us, whether it's hunting or agility or just navigating everyday life. Their ability to interpret our gestures also helps them solve problems they can't solve on their own.

COOK: I see you have created a subscription-based Web site, Dognition.com. Can you tell me about it?
HARE: Dognition is about helping people find the genius in their dog. The only way to find their genius is to compare them with other dogs. As I said, different dogs use different strategies to solve problems. Does your dog rely on you to solve problems, or are they more independent? Do they pay attention to where you are looking before they decide to sneak food off the coffee table, or are they unaware when you are watching—making it hard for them to be sneaky?

Dognition is all about playing fun games that will give you a window into your dog's mind and that will in turn enrich the relationship you have with your dog. On top of that, the data that you enter will contribute to a huge citizen science project that will help us help all dogs, from shelter dogs to service dogs. Everyone who signs into Dognition will not only get an extensive cognitive profile of their own dog, but the data will also be entered into a database that scientists can use to answer all these burning questions that we have never had the resources to answer, such as about breed differences.

The largest single dog study published tested around 15,000 dogs. With Dognition and people's input, we have the potential to test hundreds of thousands or even millions of dogs. It's an incredibly exciting project, and I can't wait to see what we find out.

COOK: Like the "yawn test"?
HARE: Even as young children, we laugh when we see someone laughing, and we cry when we see someone in distress. Our ability to "catch" the emotions of others is called emotional contagion. A common form of emotional contagion is yawning. If you see, hear or even think about someone yawning, you will probably feel an irresistible urge to yawn yourself. Contagious yawning is related to empathy scores in adults.

ONE STUDY SHOWS THAT DOGS PREFER TO SPEND TIME WITH HUMANS RATHER THAN THEIR OWN SPECIES, WHICH IS UNUSUAL FOR AN ANIMAL.

It looks like some dogs also contagiously yawn. The yawn test is just the owner yawning and seeing if their dog yawns back. It's a really simple test, but it can tell you a lot about your dog.

COOK: How empathetic are dogs, truly, when it comes to their human partners, and how much is just our imagination or our need to believe that they understand us?
HARE: As a scientist, it is hard to design tests that assess whether an animal is empathetic because most research on empathy in humans relies on people reporting how they feel, and dogs can't talk (or at least not yet in a way we can understand them). But there is definitely something special about the bond we have with dogs. Their ability to read our communicative gestures makes them seem in tune with us. And their attentiveness to our every move can't help but make us feel special. There is one study that shows that dogs would prefer to spend time with humans rather than their own species, which is unusual for an animal. Every dog owner is familiar with that rise in spirits as a thumping tail greets you at the door—and from the enthusiasm dogs have for us, it's hard to believe the feeling isn't mutual.

There are several measures, such as contagious yawning, that show that dogs probably at least have a basic form of empathy. And studies show that dogs and humans experience a rise in oxytocin, the "hug hormone," when we embrace and pet them (although it seems dogs get a higher boost in oxytocin when they are petted by women, as opposed to men).

COOK: What is the "wolf event," as you call it, and what is its significance?
HARE: The "wolf event" was a curious episode in evolutionary history when wolves basically took over Europe. Between 1.7 million and 1.9 million years ago, during one of the ice ages, the relatively small Etruscan wolf spread throughout Europe. It was also around this time that humans were emigrating out of Africa.

But the wolf's reign didn't last long. As modern humans became the dominant carnivore, we persecuted other large carnivores to extinction—which is why dogs are such an interesting puzzle. Some have proposed that modern humans adopted wolf puppies and raised them, although this doesn't really make sense. Humans have never had a particularly amicable relationship with wolves. We tend to have a low tolerance for fanged predators, and the annihilation of wolves in the past 1,000 years almost led to their extinction. Some say humans discovered that tame wolves were excellent hunting partners, but wolves eat a lot of meat. A pack of 10 would need a deer a day. And humans were successful hunters without wolves.

The puzzle is how the big bad wolf was tolerated around humans long enough to evolve into the mutt that now sleeps on the sofa. It took my childhood dog (Oreo), a Russian genius, Siberian foxes, New Guinea singing dogs, Hungarian scientists, bonobos in Congo and a decade of research for me to figure out the answer.

And the answer is ... you'll have to read the book to find out. But to give you a hint, it's not always survival of the fittest. Sometimes it's the friendliest that have an evolutionary edge. SA

Gareth Cook is a Pulitzer Prize–winning journalist who edits *Scientific American*'s Mind Matters online news column.

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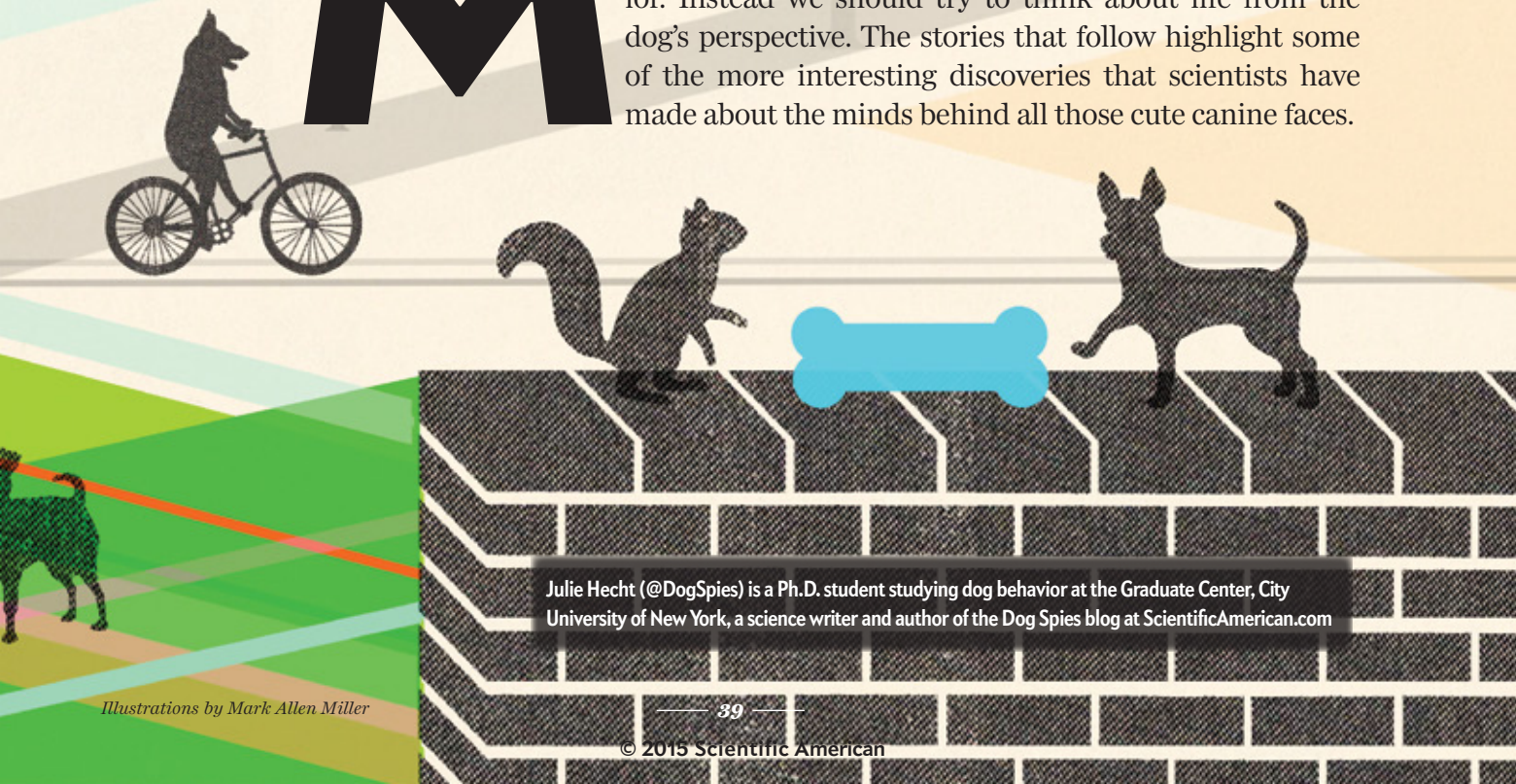
The World According to Dogs

Scientific findings uncover what our best friends know, why they do what they do and how to keep them happy

By Julie Hecht

MOST OF US DO NOT UNDERSTAND DOGS AS WELL AS WE THINK WE do. We assume we know things, but we often rely on old theories and frequently do not look at actual dog behavior. Instead we should try to think about life from the dog's perspective. The stories that follow highlight some of the more interesting discoveries that scientists have made about the minds behind all those cute canine faces.



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Illustrations by Mark Allen Miller

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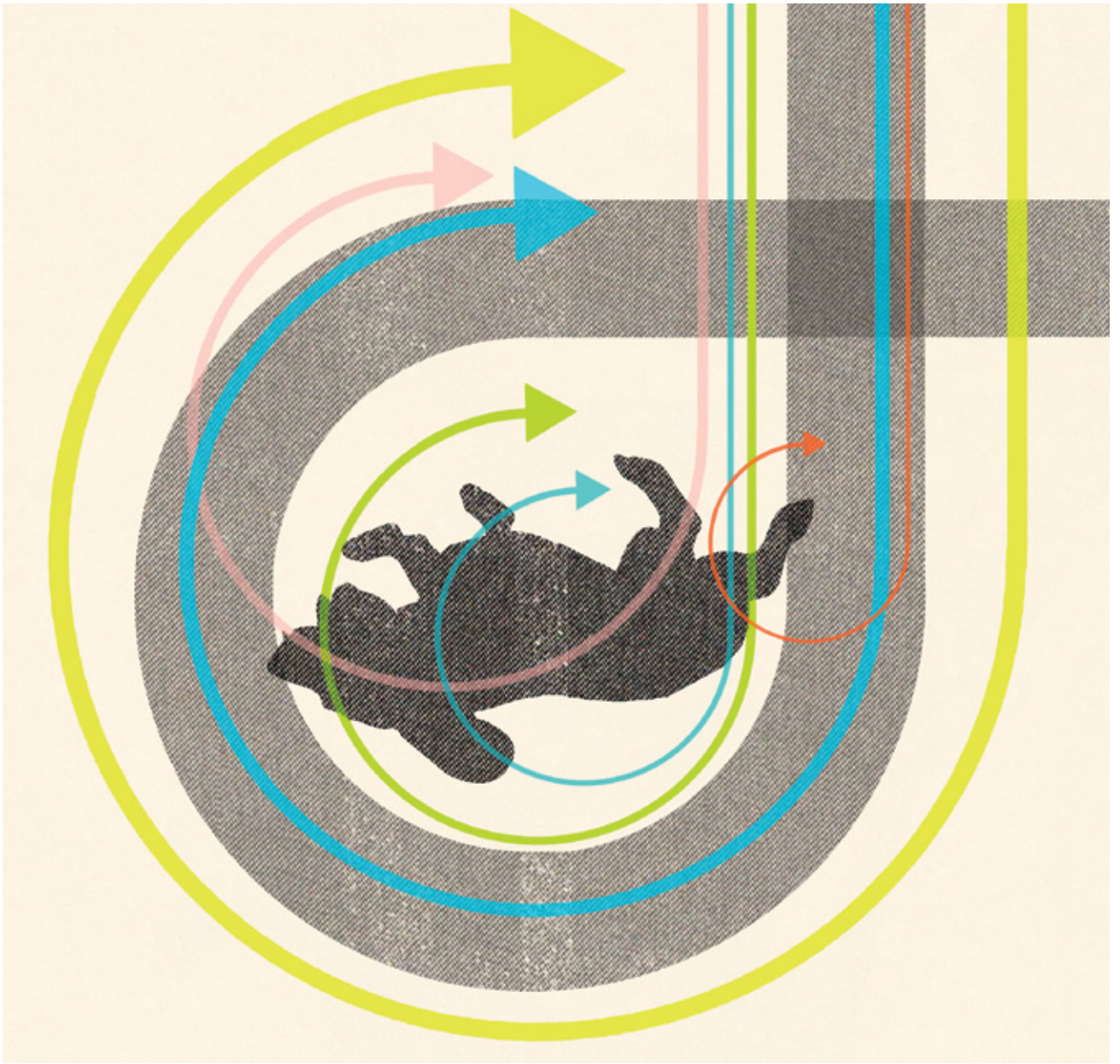
THE MEANING OF BELLY-UP

When a dog rolls onto its back during play, does the maneuver indicate submission, akin to a person crying "uncle," or does it signify something else altogether? A study published earlier this year, by Kerri Norman and her colleagues at the University of Lethbridge in Alberta and at the University of South Africa, comes down on the side of "something else."

Their report appeared in January in an issue of *Behavioural Processes* devoted to canine behavior. Investigating what behaviors mean during dog-dog play is not new. For example, you have probably heard of play signals that help dogs to clarify play from not play. These signals indicate something like, "Hey, when I just bit you in the face, I didn't mean it like 'I'M BITING YOU IN THE FACE.' It was just for fun. See! Here's a play bow for additional clarity. All fun here!" Play signals may also include exaggerated, bouncy movements or presentation of a "play face"; they start or maintain play, and they occur around potentially ambiguous behaviors—such as a bite, tackle or mount—or anything that might be misconstrued as not playing. But not all behaviors that appear during play between dogs are as well studied.

Outside of play, rolling onto one's back



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is often seen as a submissive gesture that curtails or avoids aggression by another dog. In a classic 1967 paper in *American Zoologist,* Rudolf Schenkel of the University of Basel in Switzerland describes this so-called passive submission as expressing "some kind of timidity and helplessness," like coming out with your hands up or waving a white flag.

Some have suggested that the rollover performed in dog-dog play is still about preventing aggression. Owners observing playing dogs from the sidelines often take this a step further—the dog spending more time on its back is labeled "submissive" or "subordinate," whereas the dog on the top is "dominant."

ANOTHER WAY TO THINK ABOUT ROLLING OVER IN PLAY IS AS A SELF-HANDICAPPING BEHAVIOR THAT HELPS DOGS OF DIFFERENT SIZES OR SOCIABILITIES PLAY TOGETHER.

But what if rolling over means something different during play? Norman and her colleagues wanted to know whether "rolling over onto the back and adopting a supine position" during play is an "act of submission" and serves to stop the interaction or hinder subsequent aggression. Or, they speculated, it might be essentially playful, "executed tactically, for combat purposes," to encourage play, avoid a play bite (defensive maneuver) or deliver a play bite (offensive maneuver).

They collected data in two different contexts: staged play sessions where a medium-sized female dog was paired with 33 new play partners of various breeds and sizes, and 20 YouTube videos where two dogs played together—half the videos paired similarly sized dogs, and the other half had dogs of different relative sizes.

Not all observed dogs rolled over during play, particularly in the staged play sessions, where only nine partners rolled over when playing. In the YouTube videos, 27 of the 40 dogs rolled over, and it occurred in both similarly sized and differently sized pairs. If your dog is not a roller during play, you are in good company.

For dogs that did roll over, what did it mean? The researchers examined all instances of the behavior to see whether they were associated with submission—decreasing play, remaining passive, or being performed by the "smaller or weaker" partner—or were instead associated with the interactive, fun, combative nature of play, where rollovers preceded "launching an attack (offensive), evading a nape bite (defensive), rolling in front of a potential partner (solicitation) or rolling over in a nonsocial context (other)."

The findings are stark: the smaller of the two play partners was not more likely to roll over than the larger dog. Additionally, "most rollovers were defensive and none of the 248 rollovers was submissive." Most of in-play rollovers in the study, the researchers found, were part of *play* fighting (meaning the fighting was itself playful, not *real* fighting).

But could it be that once dogs are on their back, submission kicks in? For example, a dog could go on its back to avoid a neck bite and then lie motionless, suggestive of passive submission. But that is not what the dogs did. Instead once on their back, dogs in the supine position both blocked playful bites and launched them at their partner.

Another way to think about rolling over in play is as a self-handicapping behavior that helps dogs of different sizes or sociabilities play together. Self-handicapping is instrumental to play, and it implies that a dog is tempering its behavior. For example, during play, dogs do not deliver bites at full force, and a larger dog might roll over to allow a smaller dog to jump on or mouth it. Some dogs will even use this behavior to invite bites and solicit play from another dog.

It is not safe, then, to assume that a dog sliding onto its back during play is essentially saying, "YOU CAME ON TOO STRONG" or "OKAY, YOU WON THIS ROUND!" In some contexts, this posture is certainly associated with fear or with defusing or preventing aggression, but the recent study reminds us that rolling over, as with many behaviors, does not have a single, universal meaning. Instead it is often just playful.

WHEN A DOG WON'T PLAY

YOU HAVE PROBABLY HEARD the expression, "Life is short: play with your dog." "Okay!" you think, "I'll do it!" After all, dogs play together until they are exhausted. They also play with people, although that is not always a given. Have you ever tried to play with a dog, and it just doesn't work? "The dog's not playing right," you may think. "This stinks."

Don't be so quick to blame the dog. Research suggests that it might be *you* who is not "playing right."

In 2001 animal welfare and behavior researcher Nicola Rooney, now at the University of Bristol in England, and her colleagues wanted to know whether dogs respond to people's play signals. In the study, volunteers played with their dog for five minutes in the comfort of their home, and the sessions were videotaped. Owners were asked to engage with their dog "as they usually did," but here is the key: they were not allowed to use objects or toys.

After the sessions, the researchers watched the videos and noted which behaviors owners used to initiate or maintain play. They identified 35 common play signals, including patting the floor, clapping, shoving, hitting or tapping the dog and, of course, play bowing. People also blew at dogs, barked at them and grabbed their paws. And who can forget my favorite behavior, "hand spider," where the "person moved their hand or fingers simulating movement of an insect or other creature."

Did dog owners' play signals in-

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stigate play? And more specifically, did the commonly used signals elicit play more often than the rarely used ones?

Of the 35 most common play signals, Rooney and her colleagues found that a signal's popularity "was not related to its success at initiating or sustaining play." For example, patting the floor was used most often, but play followed only 38 percent of the time. Other not so successful but commonly used invitations included scruffing the dog and clapping. Some things people did, including picking up or kissing the dog, failed to elicit play during any of the sessions.

All is not lost! A few behaviors were incredibly successful. The researchers found that giving chase and running away and lunging forward were associated with play 100 percent of the time. Signaling "up" (tapping one's chest to entice the dog to jump up), grabbing or holding a dog's paws, and play bowing also got great results.

INSTEAD OF BLAMING DOGS FOR NOT PLAYING RIGHT, PEOPLE COULD LOOK AT THEIR OWN BEHAVIOR AND EVALUATE ITS EFFECT, ACKNOWLEDGING THAT CERTAIN PLAY SIGNALS ARE MORE EFFECTIVE AT ELICITING PLAY THAN OTHERS.

The study's conclusion is somewhat somber: "We suggest that humans often use ineffective [play] signals." Instead of blaming dogs for not playing right, people could evaluate the effects of their own actions, acknowledging that certain signals are better at eliciting play than others.

Alexandra Protopopova, now at the Human-Animal Interaction Lab at Texas Tech University, and her colleagues at the Arizona State University Canine Science Collaboratory have highlighted a sad consequence of inept play signaling by humans: it can sabotage adoption of a dog from a shelter. The team found that when a potential adopter takes out a shelter dog for a one-on-one meet and greet, only two behavioral variables predicted whether that dog was leaving the shelter: lying in close proximity to the person and responding to the person's play solicitation. Dogs lying close to the person were about 14 times more likely to be adopted, and a dog who ignored a person's play initiation was unlikely to be adopted.

Taken together, these two studies paint a potentially scary picture for shelter dogs: people do not always use play signals that result in play, but people are unlikely to adopt a dog that does not respond to their signals. Nobody wins.

A subsequent study by Protopopova and her colleagues found that when potential adopters were explicitly told to play with a dog's preferred toy, not only did social play increase, but so, too, did adoption rate.

When I think about dogs in a shelter going up for their one-on-one interviews, I hope potential adopters cut them some slack and do not blame the dogs if they do not grasp overtures for play. The list of factors that could contribute to whether a dog will play with a new, strange human it just met are endless. On top of that, the shelter environment is often a weird, chaotic place, not exactly hospitable to having a fun time.

When meeting a dog for the first time, go slowly and keep your expectations in check. For shelter dogs, as with speed dating, a lot is riding on the first encounter. Reflect on your play behaviors just as much as you think about theirs.

IS THAT REALLY GUILT YOU SEE?

Live with a dog, and you have most likely met the "guilty look." You come home. The plants are knocked over, and soil is tracked all over the floor. The dog is abnormally still and averts its gaze as it thumps its tail slowly.

But does the dog feel responsible for the mess and sorry about having disobeyed your rules? That is hard to say. Research to date, including an open-access study published earlier this year, suggests that the answer is no. Moreover, the findings reveal that scolding or punishing dogs will not necessarily decrease unwanted behavior.

Owners asked to describe a dog's guilty look comment that, in addition to potentially freezing, looking away and thumping their tails, the dog may try to look smaller and assume a nonthreatening pose. Some might lift a paw or approach the owner in a low posture. Others retreat.

It is tempting to think that if a dog acts much as we do when we feel guilty, then the dog must also understand that its behavior was wrong and feel guilty. Yet these are the same actions that animal behavior researchers and experts describe as reflective of submission, appeasement, anxiety or fear. Such displays are employed by social species, such as dogs and wild gray wolves, in many different contexts to reduce conflict, diffuse tension and reinforce social bonds.

When we investigators create experiments to better understand dogs' conceptual frameworks, we often find that although their actions might look much like those of people, their understanding of a

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situation might differ. In this case, it is possible that rather than guilt operating when your dog puts on a guilty face, the pooch may actually be experiencing general anxiety or fear or a desire to avoid being on the wrong end of your anger or frustration.

In 2009 Alexandra Horowitz of Barnard College (and author of *Inside of a Dog: What Dogs See, Smell, and Know*) published a study in *Behavioural Processes* that explored the events preceding the seemingly guilty look. By varying both the dog's behavior (either eating or not eating a disallowed treat) and the owner's behavior (either scolding or not scolding), she was able to isolate what the look was associated with. She found that it did not appear more when the dogs had done something wrong. Instead it popped out in full form when the owner scolded. Horowitz further found that when dogs were reprimanded, the most exaggerated guilty look was displayed by the dogs that had not eaten the treat but were reprimanded anyway (because the owner thought the dog had eaten it). That means, for example, that in a multidog household, a dog could easily look guilty without ever having transgressed.

I found a similar result in a follow-up experiment that I conducted with Ádám Miklósi and Márta Gácsi of the Family Dog Project at Eötvös Loránd University in Budapest and published in *Applied Animal Behaviour Science* in 2012. Dogs had the opportunity to break a rule (that food on a table is for humans and not dogs) while owners were out of the room. When the owners returned, dogs that ate were not more likely to look guilty than those that abstained. In this context, the guilty look was not present without a scolding owner. We also looked at whether owners are better able than others to tell when their dogs have been disobedient. Owners who had seen their companions adhere to the rule were not better at identifying that the dogs had transgressed in their absence.

"But wait!" the peanut gallery cries. "I have seen my dog act guilty *before* it is scolded." Owners often do interpret such behavior to mean that dogs "know" they have done wrong. This is a complicated issue, but findings to date suggest that dogs engage in guilty-seeming behavior when they sense that something will elicit an owner's displeasure and hope to avoid a breach in the relationship.

Earlier this year Ljerka Ostojić and Nicola Clayton of the University of Cambridge and Mladenka Tkalčić of the University of Rijeka in Croatia reported in *Behavioural Processes* on research into whether a dog's guilty look could be triggered by environmental cues, such as the disappearance of a forbidden food. By using a manipulation somewhat similar to that of Horowitz, Ostojić and her colleagues found that the guilty look was not affected by the dog's own behavior (either eating or not eating the food) or whether the food was present or absent. In their experimental context, dogs did not display the guilty look in the absence of a scolding owner.

At the same time, the study does not exclude the possibility that in the home environment, owners may very well observe the infamous look prior to scolding. In the late 1970s a veterinarian in Wisconsin published a paper offering a clear example of fear masquerading as guilt. A dog called Nicki had taken to shredding paper in the owner's absence. To see if the dog's guilty-seeming behavior actually stemmed from guilt, the veterinarian had the owner shred paper, leave the house and return home. When the owner came back, Nicki looked "guilty," even though she had done nothing wrong. Dogs are incredibly sensitive to environmental and social cues. In this case, the dog apparently viewed the paper on the floor as a sign of a scolding to come.

SCOLDING A GUILTY-LOOKING DOG AFTER THE FACT COULD GIVE YOU A FALSE SENSE OF MUTUAL UNDERSTANDING AND THE INCORRECT BELIEF THAT YOU ARE PUNISHING THE BAD BEHAVIOR EFFECTIVELY.

"Evidence + Owner = Trouble," explains primatologist Frans B. M. de Waal, in *Good Natured: The Origins of Right and Wrong in Humans and Other Animals*. As a social species aiming to maintain relationships, dogs could show submissive displays before an owner scolds without the behavior indicating an apology or admittance of guilt. Instead these displays can aim to appease or pacify. And they certainly could have that effect: in one study, I found that nearly 60 percent of owners surveyed on a questionnaire reported that the "guilty look" led them to scold their dog less.

You may wonder why I and others harp on the misattribution of a sense of guilt in dogs. As I have said online in The Dodo, this is an issue of dog welfare: "When you get angry or forgive your 'guilty' dog for demolishing your house, you ignore deeper concerns that, if addressed, could reduce or eliminate those behavior problems. Was the dog bored? Scared? Anxious? Did something change in your routine that confused it? Sadly, scolding dogs often does not decrease future undesirable behavior. If anything, the 'guilty look' could just become more exaggerated over time as your confused companion enters an anxious cycle of destruction and appeasement."

Even worse, scolding a guilty-looking dog after the fact could give you a false sense of mutual understanding and the incorrect belief that you are punishing the bad behavior effectively. A punishment, by definition, decreases the behavior in the future. Unfortunately, studies find that scolding a "disobedient" dog, especially after it misbehaves, does not lead to a notable decrease in the "bad" behavior. A study from the late 1960s found that dogs reprimanded just 15 seconds after performing a "disallowed" behavior not only continued to perform the behavior in the future but did so while showing notable appeasement and fear-related behaviors.

Essentially beratement after the fact did not work, and the guilty look is better interpreted as fear or appeasement. Best to just clean up the mess and think about how to avoid it in the future.

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WHY DOGS LIKE PEOPLE

DO YOU EVER WONDER WHAT MAKES some dogs *so* into us? Why at any moment Pluto might propel himself into Mickey's arms, giving Mickey a full-on scrub-down with his tongue? Why some dogs want to meet everybody and anybody, whereas others would prefer you stay right where you are?

A recently published study in *PLOS ONE* led by Anna Kis, Melinda Bence and other researchers at the Family Dog Project at Eötvös Loránd University in Budapest used a novel method to explore the role that oxytocin plays in dogs' sociability toward humans.

Maybe you have heard oxytocin described as the "love hormone" because of its involvement in social interactions, stress relief and feelings of connectedness with other people. Spend time petting your dog, scratching Pluto's body and ears, and you are both apt to see increases in the oxytocin levels in your blood, indicating a positive experience for you both. Yet oxytocin is also not simple. Science writer Ed Yong points out in a 2012 Slate article: "The 'love hormone' fosters trust and generosity in some situations but envy and bias in others, and it can produce opposite effects in different people." Part of the story could be that variations in the gene that codes for the oxytocin receptor—the molecule that oxytocin binds to on nerve cells in the brain—mediate differences in social behavior.

To investigate whether Pluto's exuberance for Mickey and "people" in general is somehow associated with Pluto's genes, Kis and her colleagues took the following approach:

Step 1. Get to know the dog oxytocin receptor (*OXTR*) gene. For this study, the researchers selected dogs from two breeds, German Shepherds and Border Collies, and extracted DNA by swabbing the insides of their cheeks. This process ultimately identified three variations of the *OXTR* gene that themselves each come in two forms, with the forms seemingly having different effects on behavior. The three variations, or "polymorphisms," have the incredibly easy names of *–212AG, 19131AG* and *rs8679684*.

Step 2. Get a sense of how the dogs interact with people. More than 200 German Shepherds and Border Collies living

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as companion dogs participated in a series of specific interactions with people. The tests investigated how dogs greeted both a known and an unknown person, how dogs responded to a stranger approaching in a threatening manner, and how dogs responded when their owner hid behind a large tree.

Step 3. Bring dog genes and behavior together. The researchers examined whether there was a relation between the *OXTR* polymorphisms and the way the dogs interacted with people during the social tests. They were particularly interested in how readily dogs approached people, as well as the canines' level of friendliness.

Describing the results, Kis says "the way dogs behave toward humans, at least among German Shepherds and Border Collies, is influenced by the oxytocin receptor gene." For example, when it came to the *–212AG* gene, both German Shepherds and Border Collies carrying the form, or allele, known as *G* showed less interest in being around people, than did those with the allele called *A,* suggesting the effect was the same in both breeds.

Yet analysis of the genes *19131AG* and *rs8679684* revealed opposite trends in the two breeds. For example, in the *19131AG* polymorphism, the investigators report, "the presence of the *A* allele, as opposed to the *G* allele, was associated with higher friendliness scores in German Shepherds and lower friendliness scores in Border Collies." This opposite effect suggests that "other genetic and cellular mechanisms (unexplored in the present study) might play a role in the regulation of this behavior besides our candidate gene."

Overall, then, the study indicates that dog sociability toward people is related to the varieties in the *OXTR* gene they possess but that oxytocin is "part of a bigger system" contributing to dogs' feelings toward humans.

Next up for this line of research: replication and the exploration of possible molecular interactions that account for the effects that particular oxytocin receptor variants have on dogs' behavior toward people.

NO GUARANTEES

Does Your Pooch Love You?

The answer may surprise you

By Jason G. Goldman

You love your dog. Does your dog love you back? A group of Swedish and Danish researchers went looking for an answer. More specifically, knowing that dogs are highly attuned to cues from humans, the researchers suspected that dogs belonging to owners who felt they had a great relationship with their pets would also perceive that the relationship was close, perhaps because the owners' attitude would lead to a high frequency of positive interactions between the duo.

Twenty dog-owner pairs participated in the study, which was led by Therese Rehn of the Swedish University of Agricultural Sciences and published in the January 2014 issue of *Applied Animal Behaviour Science.* The humans all completed a questionnaire called the Monash Dog Owner Relationship Scale (MDORS), which was designed to evaluate the strength of the relationship from the perspective of the owner. The MDORS contains 28 items divided into three subscales. The first subscale assesses the nature of the dog-owner interactions ("How often do you hug your dog?"), the second reflects the emotional closeness that the owner feels toward his or her dog ("I wish my dog and I never had to be apart"), and the third concerns the perceived investment required to care for a dog ("My dog costs too much money").

The dogs were thrust into a modified version of the Ainsworth "strange situation" procedure, a clever experiment originally designed to measure the strength of human parent-child relationships. It centers on a child—or dog—being left alone with a stranger. The doggy version begins with the owner sitting in a chair ignoring the dog. After a few minutes, a stranger comes into the room and, ignoring the dog, talks to the owner. The stranger attempts to play with the dog, and then the owner quietly leaves the room. The stranger continues to engage the dog in play and then exits, leaving the dog alone. The owner returns, greets the dog and begins ignoring it again. The stranger returns, greets the dog and ignores it as well. Finally, the owner leaves once more.

When conducted with human toddlers, the slightly distressing nature of the strange situation activates an innate, adaptive system that motivates the child to seek comfort from the parent. By carefully observing the children and weighing their comfort-seeking behaviors against their more independent exploration behaviors, researchers can determine whether or not children have secure emotional attachments to their parents. Children who feel more securely attached are more likely to seek closeness with Mom or Dad when stressed but also to play independently once they feel comfortable.

The researchers predicted that canines whose owners perceived their relationship with their pets to be strongest would behave in ways indicative of strong bonding during the test. Instead they found only two significant correlations. When dogs were reunited with their owners after being alone, those whose owners reported having a lot of interactions with the animals sought out such interactions more—which might look like strong attachment but could equally have been a reflection of past rewards for initiating physical contact. And unlike securely attached toddlers, canines of such owners were less likely than others to play independently in the strange situation. In that way, they resembled insecurely attached youngsters. Dogs are not children, though, and did not show the separation anxiety that insecurely attached children display; thus, the latter finding is hard to interpret.

This study marks one of the first attempts to scientifically probe the connection between dogs' perceptions of their bond with their owners and owners' perceptions of their bond with their dogs. And here's the bad news for all those dog lovers who are just certain that Fluffy loves them back: there was no correlation between the "perceived emotional closeness" subscale of the MDORS questionnaire and the dogs' behavior in the strange situation. The researchers put it bluntly: "There was no evidence to support the view that because a person has a strong emotional bond to their dog, their dog is similarly attached to them." You cannot simply love a dog so much that it will be forced to love you back.

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BEWARE THE FEAR

KNOWING WHEN A DOG IS HAPPY IS EASY, but spotting fear is a lot harder, as Michele Wan, a certified applied animal behaviorist, and her colleagues showed in research examining whether people's perceptions of dogs' emotions vary according to experience. In the study, published in *PLOS ONE* in 2012, volunteers—who were grouped as having little or no experience with dogs, having lived with a dog at some point, or working with dogs for more or less than 10 years—watched short video clips of dogs. They then categorized the dogs' emotional state and noted which body parts tipped them off. Because the videos had no sound, participants had to rely on behavior to label a dog as, say, fearful or happy. These videos were not just any videos. They had been prescreened by dog-behavior experts whose schooling or professional experience had trained them to make science-based assessments of animal behavior.

Happy dogs proved easiest to identify. Even people with little dog experience could watch a dog frolicking in the snow or rolling joyfully on its back and describe that dog as happy.

But fear was different. Study participants who were dog professionals did a better job identifying fear compared with both dog owners and people with little dog experience. "It did not matter whether the dog professionals were relative newcomers to the field, had worked with dogs for less than 10 years, or were longtime professionals with 10 or more years of experience," Wan adds. "They had the same proficiency in identifying fear."

EVEN IF YOU LIVE WITH THE MOST HAPPY-GO-LUCKY DOG ON THE PLANET, FEAR SHOULD STILL BE ON YOUR RADAR, ESPECIALLY IF YOUR DOG INTERACTS WITH OTHER DOGS.

One reason that the dog professionals did so much better could be that they looked at more dog body parts for clues, such as the eyes, ears, mouth and tongue, whereas nonprofessionals looked at fewer body parts and were less likely to tune into dogs' facial features.

Fortunately, you can learn how to notice and interpret subtle canine behaviors. Indeed, even if you live with the most happy-go-lucky dog on the planet, fear should still be on your radar, especially if your dog ever interacts with other dogs. Recognizing fear in another dog can help you know to give that dog space; the owner can take it from there.

What does fear look like? It can include a wide variety of body parts and postures. Wan and her colleagues explain that "fearful dogs are said to reduce their body size—crouching into a low posture, flattening their ears and holding their tails in a low position. Shaking, yawning, salivation, freezing, panting, paw lifting and vocalizing are examples of other behaviors that have been associated with fear in dogs."

It is possible to help dogs become less fearful. Noticing fear and related behaviors is the first step; identifying and modifying an animal's perception of fear-inducing stimuli is just as important. Picture a dog that is afraid of new people coming to the home, everyone from the postal delivery worker to your best friend. But now, when anyone comes to the home, the dog gets pieces of its most favorite food. Through counterconditioning, visitors gradually assume a new meaning as the dog associates people coming over with a good thing, in this case yummy food. As the dog's emotions shift, so, too, does its behavior—fearful postures fade away to reveal a dog anticipating something good, a dog essentially saying, "OMG!! A NEW PERSON IS HERE!! YES!!" A happy dog is born.

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WHAT BARKS SAY

ALTHOUGH AT TIMES YOUR DOG'S VOCALIZATIONS MIGHT be unwelcome, those sounds carry much more information and meaning than you might think. In recent years many studies have investigated the noises made by companion dogs.

One major finding: dogs bark differently in various contexts, and it is possible to tell the difference. A 2004 study by Sophia Yin and Brenda McCowan in *Animal Behaviour* reported that "disturbance barks" (emitted in response to a stranger ringing the doorbell) sound different from "isolation barks" (when a dog is separated from an owner) and barks emitted during play. In each context, the acoustics differ: whereas disturbance barks are "relatively low-pitched, harsh barks with little variation in pitch or loudness," isolation barks are "higher pitched, more tonal and more frequency modulated than the disturbance barks," and play barks are "similar to the isolation barks except that they usually occurred in clusters rather than singly."

Instead of seeing barks as meaningless noise, pay attention. Banjo might be yipping because he is alone, or he may have noticed that someone uninvited is climbing in through your second-floor window.

Dog barks are full of information, but what about growls? Anna Taylor and her colleagues at the University of Sussex in England found that, unlike barks, many acoustic properties of growls in a play and aggressive context are alike. But aggressive growls were longer than play growls, and play growls had a shorter pause between growls. Although growls from different contexts can sound similar to human ears, Tamás Faragó and his colleagues at the Family Dog Project at Eötvös Loránd University in Budapest found that growls carry considerable meaning in dog-dog communication.

In a 2010 study published in *Animal Behaviour,* dogs were placed in a room with a bone; as they approached the bone, researchers played a recording of one of three different types of growls. Dogs responded to the "this is my food" growl by backing away from the bone and, for the most part, ignored the "go away stranger" and the play growls because those sounds were not relevant to the bone. All growls are not the same, and dogs know it.

Even though not all growls are associated with aggression, an aggressive growl should not be ignored. If you come across a situation where growling could be a sign of aggression, keep your cool, though. Jolanta Benal, author of the 2011 *The Dog Trainer's Guide to a Happy, Well-Behaved Pet (Quick and Dirty Tips),* reminds: if you punish a dog for growling, you are essentially punishing it for giving a warning. Growling is a form of communication related to emotional or inner states in a particular context. If you want to decrease it, think about what is prompting it. The growling itself is not a problem.

YOU CAN HELP

Wanted! Citizen Researchers

Don't let these projects pass you by

Over the past few years public participation in science projects has surged, and research involving dogs is no exception. Often the work consists of online activities, but sometimes it requires participants to go into the world, do something and report back. Here's a list of online dog science projects that will be active through 2015 and that, in most cases, anyone in the world can join. All are in English at a minimum; a few are also bilingual.

Canid Howl Project
University of Tennessee and numerous institutions
http://howlcoder.appspot.com/HowlCoder.html
This project is trying to understand the range of canid vocalizations, involving primarily wolves, dogs and coyotes. Participants help by listening to vocalizations and analyzing the recordings. Ultimately the investigators hope to understand more about the social behavior of the entire range of canid species and breeds.

Canine Microbiome and Behavior Project
Human-Animal Interaction Lab, Oregon State University
www.thehumananimalbond.com/Microbiome.html
Did you know that the thing your dog does at least once a day can help researchers learn more about the relations among gut bacteria, health and behavior? The Oregon study aims to identify microbiome behavior that could help improve the life of dogs with certain physical or behavioral disorders. Researchers are seeking samples of your dog's stool, along with information on the dog's health and behavior.

Cross-Cultural Comparison of the Attachment Bond between Humans and Pet Dogs
Human-Animal Interaction Lab, Oregon State University
www.thehumananimalbond.com/KutzlerAttachment
You may be able to help reveal similarities and differences in the attachments between pet dogs and their owners across cultures and environments. Researchers are seeking participants who are Latinos or non-Latinos living in the U.S. and Latinos living in Mexico.

Long-Term Dog Owners Survey
Animal Behaviour Cognition and Welfare Group, University of Lincoln, England
http://bit.do/longtermdogownerssurvey
Have you lived with your dog for at least three years? Your answers to the survey will offer insight into the factors that lead people and dogs to stay companions over many years.

Dog Relinquishment Survey
Animal Behaviour Cognition and Welfare Group, University of Lincoln, England
http://bit.dodogrelinquishersurvey
Scientists lack a solid grasp

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of the factors that contribute to the reasons people sometimes give up their dogs. This judgment-free study aims to better understand the motivation. If you have voluntarily given up a dog for any reason to another individual, party or organization, this project would like to hear from you.

Dog Personality Survey

Animal Behaviour Cognition and Welfare Group, University of Lincoln, England
http://uoldogtemperament.co.uk/dogpersonality
The questions investigators have about dog personality are endless. This Web site features projects aiming to identify robust personality traits in dogs and to trace their biology from the level of genes through the brain to their behavior. By exploring common core traits in dogs, researchers can work to manage problems relating to these traits.

Dog Personality and Vocalization Project

Family Dog Project, Eötvös Loránd University, Budapest
http://goo.gl/forms/ZDIXfDsr1M
Are there links among dog genetic profiles, personality and vocal behaviors? Help researchers by completing a short questionnaire about your dog's environment, personality and vocalizations. You can also elect to provide two additional pieces of information: conduct a short behavior test with your dog and report back on the result; send in a sample of your dog's saliva for DNA analysis.

Project: Your Dog, Inside and Out

Family Dog Project, Eötvös Loránd University, Budapest
http://goo.gl/forms/hGKC8tczcZ
Food hound? Activity seeker? Help researchers investigate the relation among activity level, feeding and body condition in dogs. If you like, you can add to the study of trait inheritance by (as with the previous project) providing a sample of your dog's saliva for DNA analysis.

Jealousy in Dogs

Family Dog Project, Eötvös Loránd University, Budapest
http://goo.gl/forms/3IWCBZguCe
You may have thought your dog is sometimes happy or angry, but how about jealous? The Family Dog Project questionnaire aims to gather details about jealousy in dogs, including the context in which it appears and the behaviors that express it. You can also choose to share a video in which you believe your dog is showing jealous behavior.

Is Your Dog Loud?

Family Dog Project, Eötvös Loránd University, Budapest
English: *http://goo.gl/forms/1FzM07wpsR*
German: *http://goo.gl/forms/ye7wZnIEkD*
Dutch: *http://goo.gl/forms/hdCxW5GkxV*
Italian: *http://goo.gl/forms/6JKgpwMNzH*
Spanish: *http://goo.gl/forms/mlXoMre3ZH*
Hungarian: *http://goo.gl/forms/w1blAU2Pah*
Does your dog growl, whine, bark, woof, cough or howl? Your dog's vocalizations are meaningful, and researchers want to hear all about them.

Emotional Content of Sounds

Family Dog Project, Eötvös Loránd University, Budapest
www.inflab.bme.hu/~viktor/soundrating/index.html
What do you hear in these sounds? The project, with instructions in English and Hungarian, asks participants to listen to and rate different vocalizations on how arousing they think the vocalization is and whether it seems positive or negative.

Woof!

Acoustic Engineering, University of Salford, England
www.sound101.org/woof/index.php
This project explores how people respond to dog barks. Scientists are trying to better understand how we react to everyday sounds.

Canine Behavior Assessment & Research Questionnaire (C-BARQ)

Center for the Interaction of Animals and Society, University of Pennsylvania
http://vetapps.vet.upenn.edu/cbarq
C-BARQ is a questionnaire designed to provide dog owners and professionals with standardized evaluations of canine temperament and behavior. It has been extensively tested for reliability and validity on large samples of dogs of many breeds. C-BARQ data are used by numerous researchers around the world to investigate a variety of dog-related questions, such as those related to aggression, fear and trainability, among others. Live with a dog? Add to the dataset by telling C-BARQ.

Dognition

Canines, Inc.
www.dognition.com
Participants can engage in different science-based games created by scientists, trainers and behavioral specialists. Dognition members can play the games with their dog and compare their dog's performance with that of other Dognition players. Membership requires a fee.

Co-Sleeping with Dogs

Clever Dog Lab, University of Veterinary Medicine, Messerli Research Institute, Vienna
English: https://goo.gl/5JPOzv
German: *https://goo.gl/PFjaTK*
Hungarian: *https://goo.gl/3X8MHh*
General Web site in German: *www.iswf.at/de/projekte-publikationen*
Whom do you hunker down with at night? The aim of this study is to find out more about the sleeping habits of owners and their pets, especially if you share the same bed or room (co-sleeping). Before you go to sleep tonight, consider completing this questionnaire.

Did you know that participants in dog studies tend to be women? Men should consider participating in such research, too. You could say that many canine studies are "looking for a few good men." —*J.H.*

GANDEE VASAN Getty Images

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The Ethical Dog

Looking for the roots of human morality in the animal kingdom? Focus on canines: they know how to play fair

By Marc Bekoff and Jessica Pierce

EVERY DOG OWNER KNOWS A pooch can learn the house rules—and when she breaks one, her subsequent groveling is usually ingratiating enough to ensure quick forgiveness. But few people have stopped to ask why dogs have such a keen sense of right and wrong. Chimpanzees and other nonhuman primates regularly make the news when researchers, logically looking to our closest relatives for traits similar to our own, uncover evidence of their instinct for fairness. But our work has suggested that wild canine societies may be even better analogues for early hominid groups—and when we study dogs, wolves and coyotes, we discover behaviors that hint at the roots of human morality.

Morality, as we define it in our book *Wild Justice,* is a suite of interrelated other-regarding behaviors that cultivate and regulate social interactions. These behaviors, including altruism, tolerance, cooperation, forgiveness, reciprocity and fairness, are readily evident in the egalitarian way wolves and coyotes play with one another. Canids (animals in the dog family) follow a strict code of conduct when they play, which teaches pups the rules of social engagement that allow their societies to succeed. Play also builds trusting relationships among pack members, which enables divisions of labor, dominance hierarchies and cooperation in hunting, raising young, and defending food and territory. Because this social organization closely resembles that of early humans (as anthropologists and other experts believe it existed), studying canid play may offer a glimpse of the moral code that allowed our ancestral societies to grow and flourish.

This dog is in a "play bow," indicating his desire to romp. Honest communication is a central tenet of canine society.

PLAYING BY THE RULES

WHEN CANIDS and other animals play, they use actions such as vigorous biting, mount-

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ing and body slamming that could be easily misinterpreted by the participants. Years of painstaking video analyses by one of us (Bekoff) and his students show, however, that individuals carefully negotiate play, following four general rules to prevent play from escalating into fighting.

Communicate clearly. Animals announce that they want to play and not fight or mate. Canids use a bow to solicit play, crouching on their forelimbs while standing on their hind legs (*opposite page*). Bows are used almost exclusively during play and are highly stereotyped—that is, they always look the same—so the message "Come play with me" or "I still want to play" is clear. Even when an individual follows a play bow with seemingly aggressive actions such as baring teeth, growling or biting, his companions demonstrate submission or avoidance only around 15 percent of the time, which suggests they trust the bow's message that whatever follows is meant in fun. Trust in one another's honest communication is vital for a smoothly functioning social group.

Mind your manners. Animals consider their play partners' abilities and engage in self-handicapping and role reversing to create and maintain equal footing. For instance, a coyote might not bite a smaller, weaker play partner as hard as she can, handicapping herself to keep things fair. And a dominant pack member might perform a role reversal, rolling over on her back (a sign of submission that she would never offer during real aggression) to let her lower-status play partner take a turn at "winning." Human children also behave this way when they play, for instance, taking turns overpowering each other in a mock wrestling match. By keeping things fair in this manner, every member of the group can play with every other member, developing communication skills and building bonds that keep the group cohesive and strong.

Admit when you are wrong. Even when everyone wants to keep things fair, play can sometimes get out of hand. When an animal misbehaves or accidentally hurts his play partner, he apologizes—just like a human would. After an intense bite, a bow sends the message, "Sorry I bit you so hard—this is still play regardless of what I just did. Don't leave; I'll play fair."

Adult wolves rein in their strength when playing with pups, keeping the game fun and fair for everyone.

For play to continue, the other individual must forgive the wrongdoing. And forgiveness is almost always offered; understanding and tolerance are abundant during play as well as in daily pack life.

Be honest. An apology, like an invitation to play, must be sincere. Individuals that continue to play unfairly or send dishonest signals will quickly find themselves ostracized. This has far greater consequences than simply reduced playtime; for instance, Bekoff's long-term field research shows that juvenile coyotes that do not play fair often end up leaving their pack and are up to four times more likely to die than those individuals that remain with others. Violating social norms, established during play, is not good for perpetuating one's genes.

Fair play, then, can be understood as an evolved adaptation that allows individuals to form and maintain social bonds. Canids, like humans, form intricate networks of social relationships and live by rules of conduct that maintain a stable society, which is necessary to ensure the survival of each individual.

Basic rules of fairness guide social play, and similar rules are the foundation for fairness among adults. This moral intelligence, so evident in both wild canines and in domesticated dogs, probably closely resembles that of our early human ancestors. And it may have been just this sense of right and wrong that allowed human societies to flourish and spread across the world. SA

Marc Bekoff is professor emeritus of ecology and evolutionary biology at the University of Colorado Boulder and an associate academic at the Center for Compassionate Conservation at the University of Technology, Sydney.
Jessica Pierce is a bioethicist and faculty associate at the Center for Bioethics and Humanities at the University of Colorado Denver, Anschutz Medical Campus.

MORE TO EXPLORE

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That Dog Is Too Fat

Many dogs are overweight or obese, but their owners don't seem to notice

By Julie Hecht

WE HAVE ALL MET DOGS THAT, WITH THEIR SMALL HEADS AND LARGE BODIES, BEAR a striking resemblance to the people with shrunken heads from the movie *Beetlejuice*. Some dogs naturally come with this particular head-to-body ratio, but for others, it is man-made.

In the 2014 book *Dilemmas in Animal Welfare,* Peter Sandøe, professor of bioethics at the University of Copenhagen, and his co-authors estimate that about one third of companion dogs in developed countries are overweight. On top of that, they suggest, "more than one in 20 is obese."

As with people, being too fat increases a dog's risk of diabetes, heart disease and other ills.

KEN BLAZE *Alamy*

And yet people often do not realize that their dogs are hauling too many pounds. In a study published in 2011, University of Nottingham researchers asked owners to categorize their dogs as underweight, normal, overweight or very overweight. Owner assessments were then compared with the judgments of veterinarians, a population specifically trained in this critical assessment of animal well-being.

How did owners do? They did know numbers! Almost 70 percent offered an estimate, suggesting they were at least somewhat familiar with their pet's weight. But they did not always understand what that figure meant for the animal's health. In fact, owners tended to underestimate whether dogs were too heavy. For example, almost 40 percent of owners with a dog deemed overweight by a veterinarian described the poundage as normal (and one owner even thought their overweight dog should gain more!). Although some owners did acknowledge that their dogs were overweight, the veterinarians often labeled these dogs as very overweight, whereas the owners tended to classify them as simply overweight.

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Canine obesity is not a joking matter, and it often impairs welfare and quality of life. Obese dogs face a higher risk of serious health problems such as diabetes, cardiovascular issues, and joint and bone disorders, as well as shortened life span (typically by about two years). In the U.K., the Royal Society for the Prevention of Cruelty to Animals (RSPCA) adds that overfeeding can be "just as cruel as underfeeding."

Is it really possible that some owners do not realize their pets are overweight? When researchers investigated the disconnect between owner and veterinarian weight assessments, they learned that the former sometimes had misguided ideas about what made up weight. For example, an owner might not consider a dog fat but rather "all muscle" (something you might imagine us saying about ourselves). Others reasoned that because Rover had lost weight, he was now good to go—although the veterinarians would still consider the animal to be overweight.

HOW TO SPOT EXCESS WEIGHT

ANOTHER POSSIBILITY is that owners simply do not know how to assess their dog's body condition. After all, what constitutes overweight versus very overweight for a particular dog?

The good news is that anyone can easily learn to evaluate a dog's body condition. Veterinarians often rely on 5- or 9-point body condition scales where dogs are examined and ranked from underweight to markedly overweight and everything in between. These tools help determine whether a dog is a healthy size or not. The American Society for the Prevention of Cruelty to Animals (ASPCA) recommends the Body Condition Tools from Purina, which offer overhead and side views of each weight category, for both dogs and cats. Looking down at your dog from above, do you see an "hour-glass" indentation near the waist? Can you feel the ribs, easily? If this is not what you feel and observe, you could have a dog that stands to lose a few.

Fat dogs do not happen overnight. In fact, they happen over many nights, as was highlighted in the first episode of a wonderful series called *Dogs: Their Secret Lives* that aired in the U.K. in 2014. That episode, "Fat Dogs," traced the way three dogs put on their extra pounds and their roads to taking them off. A hidden camera revealed, for instance, that one of them, a Cavalier King Charles spaniel named Chancer, perked up whenever Grandma ate. Grandma, it turned out, was generous to both her two- and four-legged grandchildren!

Decreasing a dog's weight after a lifetime of reinforced overeating is not easy. On eating habits in dogs, illustrator Mark Ulriksen notes—in his book *Dogs Rule, Nonchalantly* (Goff Books, 2014)—"Each of my dogs had their own favorite meal.... Though I've yet to meet a dog that's a fussy eater." Dogs like to eat. People like to feed them.

That said, being overweight is not necessarily a permanent condition. After identifying the many factors (and people) that contribute to a dog's high poundage, it is possible to reverse course. For example, in "Fat Dogs," Chancer's family learned that feeding is not just about what goes down, it's also about how it goes down. Enter puzzle toys and slow feeders; these devices can force dogs to work at getting their food, which stretches out meals and can prevent scarfing and overeating. Slow feeders can be useful for normal-sized dogs as well as those who are overweight. Of course, consulting a veterinarian or specialist is a good first step if you have questions about your dog's weight.

I can pretty much guarantee that dogs are unlikely to wake up one morning, reflect on their expanding midsection and proclaim, "Ya know, there's really no need to keep eating like this. I'm going to cut back." Instead it takes diligent pet parents to figure out what is contributing to a dog's weight gain and commit to a diet and exercise plan for improved health. This might just be an area where dogs and humans are in a similar boat.

Julie Hecht is a Ph.D. student studying dog behavior and writes the Dog Spies blog at ScientificAmerican.com

TAKE CARE

The Dog Killer in Your Pocket

Here's another danger that might surprise you

Just as dog owners often don't realize their canine friends are too heavy, they may have a blind spot about another threat. Surprisingly, the lowly penny can become a lethal weapon against dogs—specifically pennies minted after 1982.

Although all pennies are equal in value—one cent, no matter what year it is—their compositions are not. Pennies that were produced between 1962 and 1982 are predominantly copper (95 percent), whereas pennies churned out in 1982 and after are mostly zinc (97.5 percent).

Zinc is an essential mineral but is undesirable in excessive amounts. When pennies meet the acid in a dog's stomach, the zinc gets released rapidly, which can destroy red blood cells and, in turn, lead to a number of debilitating conditions, including kidney or liver damage.

Certainly no one was thinking about dogs when the U.S. Mint approved the transition from a copper to a zinc penny. But if Abraham Lincoln were alive today, I'm sure he would say, "One score and thirteen years ago, our fathers brought forth on this continent a new penny, conceived in zinc. So, please, keep them out of reach of your dogs." —*J.H.*

MORE TO EXPLORE

Canine Obesity: Is There a Difference between Veterinarian and Owner Perception? G. A. White, P. Hobson-West, K. Cobb, J. Craigon, R. Hammond and K. M. Millar in *Journal of Small Animal Practice,* Vol. 52, No. 12; pages 622–626; 2011.

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Body Condition Tools for dogs and cats can be found on the Purina Web site: www.purina.co.uk

RSPCA pet care and pet obesity: www.rspca.org.uk/adviceandwelfare/pets/general/obesity

scientificamerican.com/magazine/sa

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Cancer

IMAGINE A 60-YEAR-OLD MAN recuperating at home after prostate cancer surgery, drawing comfort from the companionship of the aged Golden Retriever at his side. What the man probably does not realize, though, is that pet dogs like his could be important players in efforts to eliminate the suffering and death caused by cancer.

Dogs and humans often fall ill with the same kinds of cancers. Scientists contend that the similarities between these tumors, including genetic resemblances, can be instructive. (The background represents the DNA sequence from a tissue sample.)

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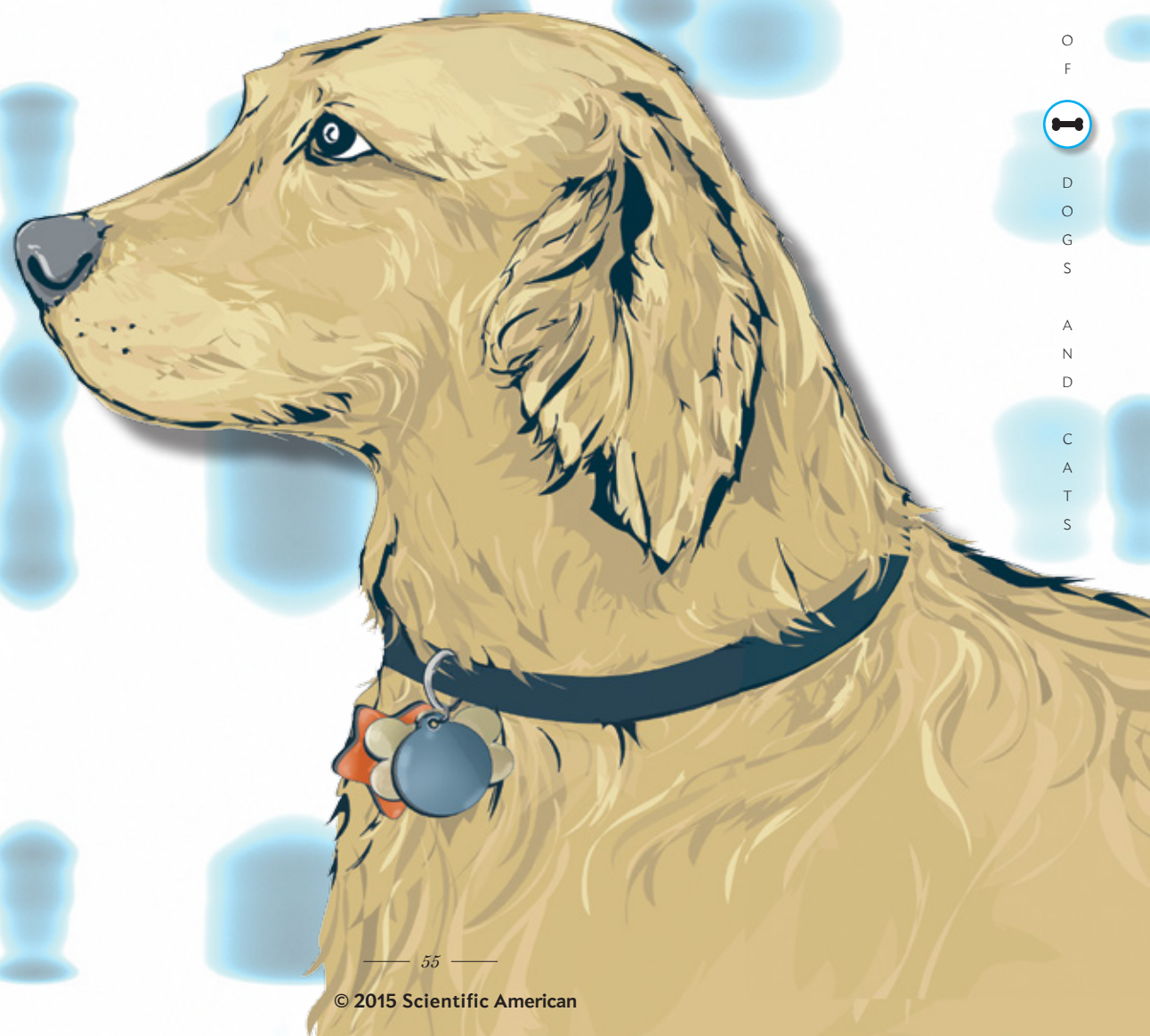
Clues from Pet Dogs

Cancer studies in dogs can offer unique help in the fight against human malignancies while also improving care for our pets

By David J. Waters and Kathleen Wildasin



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Defeating cancer will require the application of everything in investigators' tool kits, including an openness to new ideas. Despite an unprecedented surge in researchers' understanding of what cancer cells can do, the translation of this knowledge into saving lives has been unacceptably slow. Investigators have discovered many drugs that cure artificially induced cancers in rodents, but when the substances move into human trials, they usually have rough sledding. The rodent models called on to mimic human cancers are just not measuring up. If we are going to beat cancer, we need a new path to progress.

Now consider these facts. More than a third of American households include dogs, and scientists estimate that some four million of these animals will be diagnosed with cancer this year. Pet dogs and humans are the only two species that naturally develop lethal prostate cancers. The type of breast cancer that affects pet dogs spreads preferentially to bones—just as it does in women. And the most frequent bone cancer of pet dogs, osteosarcoma, is the same cancer that strikes teenagers.

Researchers in the field of comparative oncology believe that such similarities offer a novel approach for combating the cancer problem. These investigators compare naturally occurring cancers in animals and in people—exploring their striking resemblances as well as their notable differences.

Right now comparative oncologists are enlisting pet dogs to tackle the very obstacles that stand in the way of achieving a cure for cancer. Among the issues on their minds are finding better treatments, deciding which doses of medicines will work best, identifying environmental factors that trigger cancer development, understanding why some individuals are resistant to malignancies and figuring out how to prevent cancer. Comparative oncologists ask, Why not transform the cancer toll in pet dogs from something that is only a sorrow today into a national resource, both for helping other pets and for aiding people?

WHY ROVER?

FOR DECADES, scientists have tested the toxicity of new cancer agents on laboratory beagles before studying the compounds in humans. Comparative oncologists have good reason to think that pet dogs with naturally occurring cancers can likewise become good models for testing the antitumor punch delivered by promising treatments.

One reason has to do with the way human trials are conducted. Because of the need to ensure that the potential benefits of an experimental therapy outweigh the risks, researchers end up evaluating drugs with the deck stacked against success; they attempt to thrash bulky, advanced cancers that have failed previous treatment with other agents. In contrast, comparative oncologists can test new treatment ideas against early-stage cancers—delivering the drugs just as they would ultimately be used in people. When experimental drugs prove helpful in pets, researchers gain a leg up on knowing which therapies are most likely to aid human patients. So comparative oncologists are optimistic that their findings in dogs will be more predictive than rodent studies have been and will help expeditiously identify those agents that should (and should not) be tested in large-scale human trials.

Pet dogs can reveal much about human cancers in part because of the animals' tendency to become afflicted with the same types of malignancies that affect people. Examples abound. The most frequently diagnosed form of lymphoma affecting dogs mimics the medium- and high-grade B cell non-Hodgkin's lymphomas in people. Osteosarcoma, the most common bone cancer of large- and giant-breed dogs, closely resembles the osteosarcoma in teenagers in its skeletal location and aggressiveness. Under a microscope, cancer cells from a teenager with osteosarcoma are indistinguishable from

a Golden Retriever's bone cancer cells. Bladder cancer, melanoma and mouth cancer are other examples plaguing both dog and master.

In a different kind of similarity, female dogs spayed before puberty are less prone to breast cancer than are their intact counterparts, much as women who have their ovaries removed, who begin to menstruate late or who go into menopause early have a reduced risk for breast cancer. But biology is teeming with trade-offs, and investigators are now recognizing that the biological factors that seem to protect women and dogs from breast cancer may come at the cost of accelerated aging and shortened longevity.

Canine cancers also mimic those of humans in another attribute—metastasis, the often life-threatening spread of cancer cells to distant sites throughout the body. Solving the mystery of how tumor cells metastasize to particular organs is a top research priority. When certain types of cancers spread to distant organs, they tend to go preferentially to some tissues over others, for reasons that are not entirely clear. Because metastasis is what accounts for most deaths from cancer, researchers would very much like to gain a better understanding of its controls. Studies in pet dogs with prostate or breast cancer might prove particularly useful in this effort because such tumors frequently spread in dogs as they do in humans—to the skeleton.

IN BRIEF

Millions of pet dogs will have cancer diagnosed this year. In many of those animals, the malignancy will look and behave much as it would in humans, such as spreading to the same organs. **Investigation of these cancers** can help researchers to better understand the biology of the human forms. Also, studies of experimental treatments in the animals can indicate which therapies most deserve further testing in dogs and humans and can offer guidance on the best doses and methods of delivery. **Such studies could lead** to progress in cancer prevention and therapy for both pets and people.

PRECEDING PAGES: ALISON KENDALL (*illustration*); MEHAU KULYK *Science Source* (*DNA autoradiogram*); THIS PAGE: JANA BRENNING (*dog tag*)

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Breeds at Risk

The breeds represented by the dogs shown here are particularly susceptible to cancers that also afflict humans. These malignancies look like the human forms under a microscope and act similarly as well. Such resemblances mean that canine responses to experimental drugs should offer a good indication of how the compounds will work in humans. In addition, research into the genes that increase susceptibility of specific breeds to particular cancers is expected to help pinpoint susceptibility genes in humans.

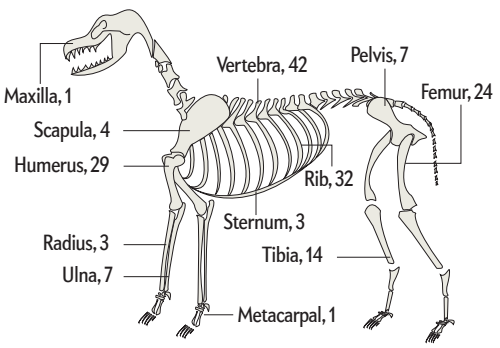
Rottweiler:
Bone cancer

Collie:
Nasal cancer

Chow Chow:
Stomach cancer

Golden Retriever:
Lymphoma

Boxer:
Brain cancer



Skeletal distribution of metastases is another aspect of cancer similar in dogs and humans. In dogs, the lesions display the same "above the elbow, above the knee" pattern seen in people. Insights into why that pattern occurs in dogs could help explain the distribution in humans and perhaps suggest new ideas for intervening. (The numerals indicate the number of metastases found at each site in one study.)

Scottish Terrier:
Bladder cancer

CORBIS (*dogs*); DANIELA NAOMI MOLNAR (*dog skeleton*). SOURCE: DAVID WATERS

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Scientists also have deeper theoretical grounds for thinking that pet dogs are reasonable models for human cancer. Evolutionary biologists note that dogs and humans are built like Indy race cars, with successful reproduction as the finish line. We are designed to win the race, but afterward it does not matter how rapidly we fall apart. This design makes us ill equipped to resist or repair the genetic damage that accumulates in our bodies. Eventually this damage can derange cells enough to result in cancer. In the distant past, our human ancestors did not routinely live long enough to become afflicted with age-related cancers. But modern sanitation and medicine have rendered both longevity and cancer in old age common. Much the same is true for our pets. Pet dogs, whom we carefully protect from predation and disease, live longer than their wild ancestors did and so become prone to cancer in their later years. Thus, when it comes to a high lifetime risk for cancer, pets and people are very much in the same boat.

Aside from acquiring cancers that resemble those in people, pet dogs are valuable informants for other reasons. Compared with humans, they have compressed life spans, so scientists can more quickly determine whether a new prevention strategy or therapy has a good chance of improving human survival rates. Finally, although veterinarians today are far better equipped to treat cancer than they used to be, the standard treatments for many canine tumors remain ineffective. Because most pet cancer diagnoses end in death, dog owners are often eager to enroll their animals in clinical trials that could save their pets' life—and possibly provide the necessary evidence to move a promising therapy to human clinical trials.

LAB RATS

The Ideal Animal Model: An Invalid Concept

Some experts contend that progress toward finding cancer cures has been frustratingly slow because of the inadequacy of available animal models of human cancer. But perhaps the problem is not in the animals themselves but in the way they are used and what we are forcing them to tell us.

The dictionary defines a model as "an imitation." By definition, therefore, an animal model of cancer is not the same as a person who acquires cancer. Rodent models are often produced by making "instant cancers"—that is, by injecting the animals with tumor cells or bombarding them with carcinogen doses that are higher than any human will ever encounter. It is doubtful that cancers produced in that way will accurately recapitulate a complex process that often requires more than 20 to 30 years to develop in people. Naturally occurring animal tumors, such as those affecting pet dogs, provide the opportunity to study this complexity in a less artificial way.

But no one animal model is capable of answering all the important questions related to the prevention or treatment of a particular type of human cancer. Researchers would be best served by turning their attention toward carefully crafting specific questions and letting the questions drive the selection of the model system. For some questions, cell culture or rodent studies will be appropriate. To answer others, researchers will have to resort to studying humans. In that sense, a human clinical trial is a form of animal model research—a specific collection of individuals is being used to represent the overall human population. *—D.J.W.*

Rodents are a favorite model of cancer researchers, but therapies that work beautifully in rats and mice often fail in humans.

ADVANCING CANCER THERAPY

VARIOUS CANCER treatment studies featuring pet dogs have now been carried out or begun. Some of the earliest work focused on saving the limbs of teenagers with bone cancer. Thirty years ago a diagnosis of osteosarcoma in a youngster meant amputation of the affected limb, ineffective or no chemotherapy (drugs administered into the bloodstream to attack tumors anywhere in the body), and almost certain death. Today limb amputation can be avoided by chiseling out the diseased bone tissue and replacing it with a bone graft and metal implant—a process partially perfected in pet dogs by Stephen Withrow and his colleagues at Colorado State University. Withrow's team pioneered technical advances that reduced the likelihood of complications, such as placing bone cement in the marrow space of the bone graft. The researchers also showed that preoperative chemotherapy delivered directly into an artery could convert an inoperable tumor into an operable one. The group's work is credited with significantly increasing the percentage of teenagers who today can be cured of osteosarcoma.

Although a tumor's local effects are often controllable using surgery or radiation, metastasis is much harder to combat. For that, drug therapy is required. New compounds under development aim to disrupt key cellular events that regulate the survival and proliferation of metastatic tumor deposits as well as their sensitivity to cancer-fighting drugs. For example, researchers are testing experimental agents that inhibit the formation of new blood vessels, which foster tumor

PASCAL GOETGHELUCK *Science Source*

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Comparative oncologists ask,
Why not transform the enormous
amount of cancer in pet dogs into
a national resource, both for
helping other pets and aiding people?

growth and metastasis. Early trials in humans and dogs, conducted in parallel, can provide a deeper understanding of cancer-fighting mechanisms and help to identify the clinical settings in which these agents will be most effective.

Cancer researchers are also turning their attention to more familiar kinds of pharmaceuticals, including nonsteroidal anti-inflammatory drugs (NSAIDs), the class of compounds that includes ibuprofen. Certain NSAIDs have exhibited significant antitumor activity against a variety of canine tumors. In studies of pet dogs with bladder cancer, for example, the NSAID piroxicam showed such impressive antitumor activity that the results paved the way for human clinical trials of other NSAIDs (for example, the cyclooxygenase-2 inhibitor celecoxib) that can amplify the effects of conventional chemotherapy drugs.

Developing new cancer therapies is not just about finding novel drugs. It is about optimizing drug delivery to the patient. In your vein or up your nose? That is the kind of information scientists testing new agents against lung cancer need to know. If the right amount of drug does not make it to the tumor, then even substances with impressive credentials for killing tumor cells in a petri dish will not stand a chance of working in human patients. Moreover, delivering pharmaceuticals directly to the target—so-called regional therapy—has the added benefit of avoiding the toxicity associated with systemic therapy.

Investigators have used pet dogs to study the intranasal delivery of a cytokine, a small immune system molecule, called interleukin-2 (IL-2) to treat naturally occurring lung cancers. Positive results from these experiments led to feasibility trials of inhaled IL-2 in human patients with lung metastases, further leading to trials with another cytokine, granulocyte colony stimulating factor. Pet dogs can also aid researchers in optimizing the dosing and delivery protocols for drugs that have already made their way into human trials.

Another challenge that pet dogs are helping to overcome is determining the extent of tumor spread, referred to as clinical staging. Accurate staging is critical for devising therapeutic game plans that will maximally benefit the patient while minimizing exposure to harsh treatments that are unlikely to help at a given disease stage. For example, the odds that a teenager will survive osteosarcoma are increased by accurate identification (and subsequent surgical removal) of lung metastases.

Doctors typically determine the presence and extent of such metastases with noninvasive imaging techniques, such as computed tomography (CT). To assess how accurate such scanning is, one of us (Waters), along with investigators at the Indiana University School of Medicine, collected CT images of the lungs from pet dogs with metastatic bone cancer and then examined the tissue at autopsy to verify that what was interpreted as a "tumor" on the scan really was a tumor and not a mistake. Results showed that state-of-the-art imaging with CT—the same type used in clinical staging of bone cancer in teenagers—significantly underestimates the number of cancer deposits within the lung. By revealing the limited accuracy of existing and experimental techniques, pet dogs are helping optimize the next generation of technologies for improved cancer detection.

TAKING AIM AT CANCER PREVENTION

BUT CANCER researchers are shooting for more than improved detection and better treatment; they also want to prevent the disease. Surprisingly, prevention is a relatively new concept within the cancer research community. What cardiologists have known for a long time—that millions of lives can be saved through the prevention of heart disease—is just now gaining traction in the cancer field. The term "chemoprevention" was coined almost 40 years ago to refer to the administration of compounds to prevent cancer, but scientists did not gather nationally to debate cutting-edge knowledge of cancer prevention until October 2002.

Today the pace is quickening as investigators are examining a diverse armamentarium of potential cancer-protective agents. But finding the proper dose of promising agents has always been challenging. Indeed, failure to do so proved disastrous for some early human trials of preventives. For example, in two large lung cancer prevention trials, people receiving high doses of the antioxidant nutrient beta-carotene had an unexpected *increase* in lung cancer incidence compared with placebo-treated control subjects.

Can dogs accelerate progress in cancer prevention? Canine studies have already helped define the dose of an antioxidant—the trace mineral selenium—that minimizes cancer-causing genetic damage within the aging prostate. The message from the dogs: when it comes to taking dietary supplements such as selenium to reduce your cancer risk, more of a good thing is not necessarily better. Elderly dogs given moderate doses ended up with less DNA damage in their prostates than dogs given lower or higher amounts. Comparative oncologists hold that dog studies conducted before large-scale human prevention trials are initiated can streamline the process of finding the most effective dose of cancer preventives and can enable oncologists to lob a well-aimed grenade at the cancer foe.

Pet dogs can assist in preventing human cancers in another way. For years

JANA BRENNING

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dogs in the research laboratory have advanced understanding of the acute and long-term effects of high doses of cancer-causing chemicals. But pet dogs, just by going about their daily lives, could serve as sentinels—watchdogs, if you will—to identify substances in our homes and in our backyards that are carcinogenic at lower doses. If something can cause cancer, the disease will show up in pets, with their compressed life spans, well before it will in people.

Take asbestos. Most human cases of mesothelioma (a malignancy of tissues lining the chest and abdomen) stem from asbestos exposure. Symptoms can appear up to 30 years after the incriminating exposure. Investigators have now documented that mesothelioma in pet dogs is also largely related to encountering asbestos, most likely through being near a master who came into contact with it through a hobby or work. But in dogs, the time between exposure and diagnosis is comparatively brief—less than eight years. So the appearance of the cancer in a dog can alert people to look for and remediate any remaining sources of asbestos. Also, closer monitoring of exposed individuals might lead to earlier diagnosis of mesothelioma and render these cancers curable.

Pet dogs could assist in discovering other environmental hazards. Some well-documented geographic "hot spots" show an unusually high incidence of certain cancers. For example, women living in Marin County, California, have a particularly high breast cancer rate. Scientists typically try to identify the factors contributing to cancer in hot spots by comparing the genetics and behavior of people who become afflicted and those who do not. To advance the effort, comparative oncologists are establishing cancer registries for pet dogs in those areas. If both pets and people living in a particular community experience higher-than-normal cancer rates, the finding would strengthen suspicions that these malignancies are being triggered by something in the environment.

Analyzing tissues of dogs could even potentially speed identification of the specific hazard. Many toxic chemicals, such as pesticides, concentrate themselves in body fat. So it might make sense to collect tissues from dogs during common elective surgical procedures (for example, spaying) or at autopsy. Later, if an unusually high number of people in an area acquire a certain form of cancer, investigators could analyze levels of different chemicals in the samples to see if any are particularly prominent and worth exploring as a contributing factor.

WHY UNCLE BILL AVOIDED CANCER

BECAUSE CANCER in pet dogs is so commonplace, the animals might be able to assist in solving an age-old mystery. Almost everyone has an Uncle Bill who smoked two packs a day and never got lung can-

DENISE M. PATTON Getty Images (Rottweiler)

LONGEVITY

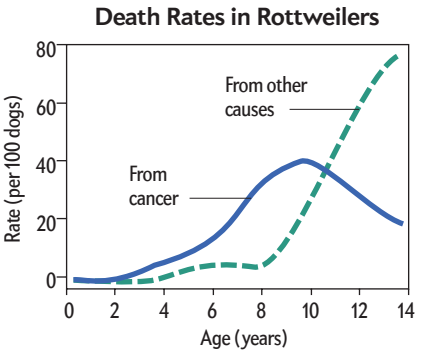
Cancer Resistance: Lessons from the Oldest Old

The risk of most human and canine cancers increases dramatically with age. This pattern has led to the belief that cancer is simply the result of a time-related accumulation of genetic damage. But recent studies of people who live to be 100 years old (centenarians) reveal an intriguing paradox: the oldest old among us are much less likely to succumb to cancer than are people who die in their 70s or 80s. Do the oldest-old pet dogs share a similar resistance to cancer mortality?

To answer this question, my colleagues and I consulted pet owners and veterinarians to construct lifetime medical histories of a large cohort of rottweiler dogs living in North America. We found that the likelihood of dying from cancer within two years rose with age during adulthood until dogs reached about 10 years but then declined after that. Moreover, exceptionally old dogs (those older than 13 years) were much less likely to die of cancer than were dogs with usual longevity even though the risk of dying from other causes continued to rise.

These findings raise the exciting possibility that studies comparing oldest-old dogs to those with usual longevity might reveal genes that regulate cancer resistance. Gene variations (so-called polymorphisms) responsible for cancer resistance and exceptional longevity in dogs could then be evaluated to see whether they are also overrepresented in the oldest-old humans. If they are, scientists can try to learn how the molecular interactions regulated by these genes alter cancer susceptibility at the tissue level.

At present, the precise nature of cancer resistance in human centenarians is poorly defined. Detailed autopsy studies of oldest-old dogs are currently under way to explore this issue. These studies should determine whether cancer resistance reflects a complete suppression of the biological events that give rise to cancer—for example, through increased repair of DNA damage—or whether tumors actually arise but are of the nonlife-threatening variety. By better understanding the genetic and pathological basis of cancer resistance in the oldest old, scientists will be better positioned to develop practical interventions that will reduce the average person's cancer risk. —*D.J.W.*



In Rottweilers who live past 10 years, getting older means having better odds of avoiding death from cancer.

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cer. So what factors determine cancer resistance? One way to tease out the answer is to find populations resistant to cancer and study them closely—their genetics, their diet and their lifestyle.

Such a population has been found—human centenarians. It turns out that most folks who live to be 100 die of disorders other than cancer. But it is nearly impossible to collect reliable information from a 102-year-old woman on her dietary habits and physical activity when she was a teenager or in her mid-40s. So Waters asked a simple question: Is this phenomenon of cancer resistance in the oldest old operational in pet dogs? The answer is yes [*see box on opposite page*]. Now by interviewing owners of very old pet dogs, comparative oncologists can construct accurate lifetime histories of "centenarian" dogs. Combine this prospect with the ability to collect biological samples (such as blood for genetic analysis and for tests of organ function) from very old dogs as well as from several generations of their offspring, and you have a unique field laboratory for probing the genetic and environmental determinants of cancer resistance.

The puzzle of cancer resistance can also be addressed in another way—by examining differences in cancer susceptibility between dogs and humans. In people, obesity and diets rich in animal fat are known to increase risk for colon cancer. In contrast, colorectal cancer in dogs is uncommon, even though many pet dogs are obese and consume a high-fat diet. Scientists are now contemplating the use of dogs as a "negative model" of colon cancer in the hope of identifying factors able to confer cancer resistance to people whose style of living strongly favors colon cancer development. Knowledge of resistance factors could suggest new interventions for nonresistant individuals.

A GROWING EFFORT

HISTORICALLY, comparative oncology research has been conducted in university-based hospitals and laboratories where veterinary oncologists are trained. But other organizations have begun to recognize the potential for this kind of research to translate into better care for people, and these institutions are now actively engaged in comparative oncology research.

The Gerald P. Murphy Cancer Foundation began in 2001 to accelerate the discovery of improved methods for preventing and treating prostate and bone cancers affecting both people and pets. To better understand the cancer-aging connection, the foundation's Center for Exceptional Longevity Studies has developed a database of more than 300 canine centenarians, focusing on uncovering the mechanisms of the cancer resistance that characterizes these longest-lived dogs. And in 2003 the National Cancer Institute developed the Comparative Oncology Program, which designs trials involving dogs and other pets with naturally occurring cancers and provides researchers with high-quality, canine-specific reagents needed for in-depth studies of the molecular biology, protein chemistry and genetics of dog tumors.

Moreover, the sequencing of the canine genome is now complete. Discovery that a particular gene is involved in some form of cancer in dogs will enable investigators to determine whether—and how—the same gene operates in human cancers. Scottish Terriers with bladder cancer, Rottweilers with bone cancer and Golden Retrievers with lymphoma—each breed can help elucidate the calamitous combinations of genes and environment that lead to cancer.

Of course, there are limitations inherent in the use of animals to mimic human cancer—whether you are talking about rodents, dogs or other species. No single, ideal animal model for cancer exists [*see box on page 58*]. The best science is done by asking good questions and then using the research tools most likely to yield meaningful answers. At times, following that rule in cancer research will mean turning to dogs to track down that hard-to-win knowledge.

Pet dogs could serve as sentinels—watchdogs, if you will—to identify substances in our homes and backyards that are carcinogenic.

The intriguing similarities between the cancers of people and pets—once a mere curiosity—are now being systematically applied to transform cancer from killer to survivable nuisance. Comparative oncologists are not inducing cancer in animals but are compassionately treating pet dogs suffering from the same kinds of lethal cancers that develop naturally in both man and man's best friend. They are putting our canine companions on the trail of a killer in ways that can save both pets and people. SA

David J. Waters and **Kathleen Wildasin** share an interest in stimulating fresh thinking about cancer. Waters is director of the Center for Exceptional Longevity Studies at the Gerald P. Murphy Cancer Foundation in West Lafayette, Ind. He earned his B.S. and D.V.M. at Cornell University and his Ph.D. at the University of Minnesota. Wildasin is a Kentucky-based medical and science writer.

MORE TO EXPLORE

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JANA BRENNING

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Making Sense of Cats

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Illustration by Bomboland

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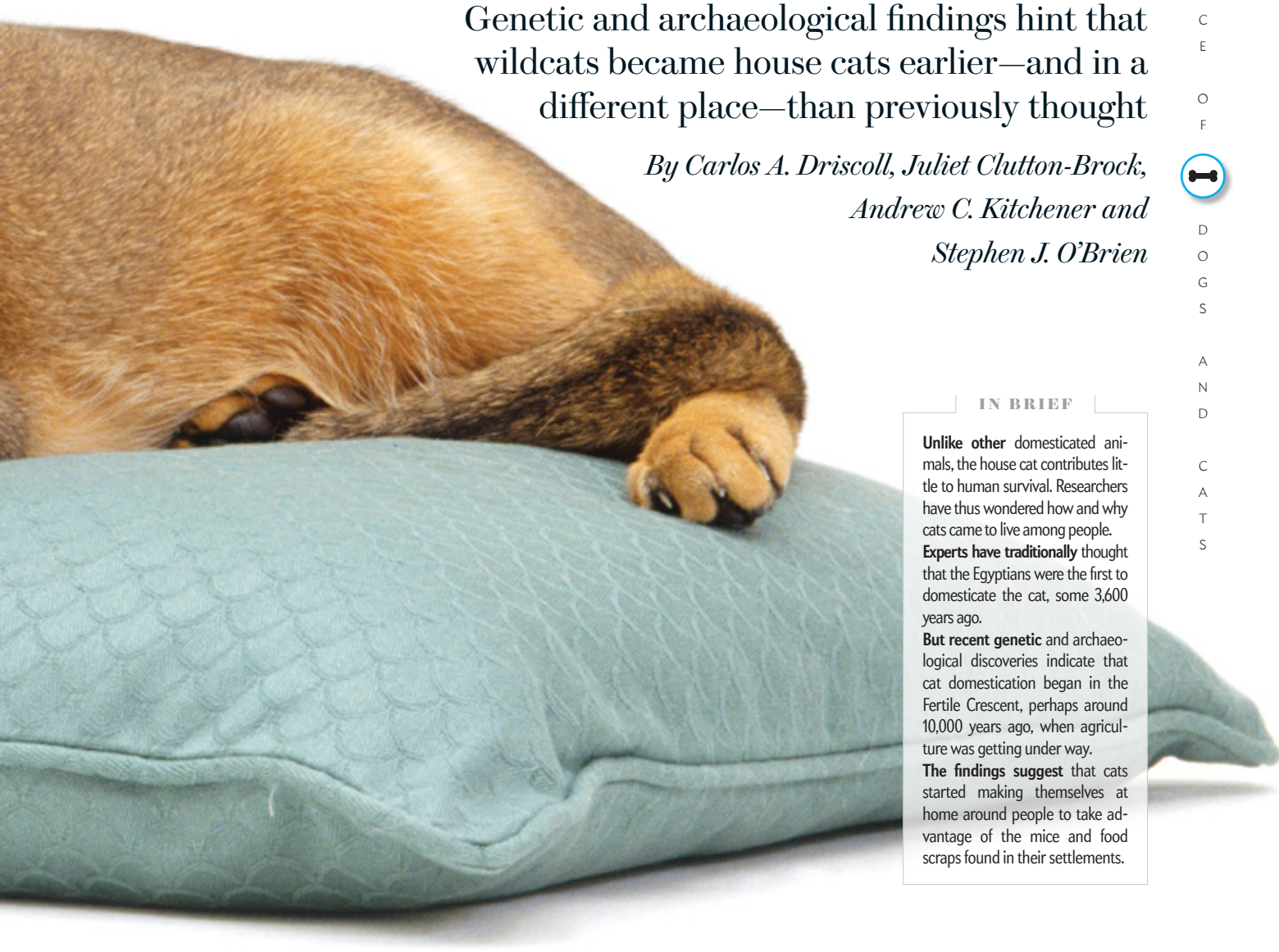
The Taming of the Cat

Genetic and archaeological findings hint that wildcats became house cats earlier—and in a different place—than previously thought

By Carlos A. Driscoll, Juliet Clutton-Brock, Andrew C. Kitchener and Stephen J. O'Brien



IN BRIEF

Unlike other domesticated animals, the house cat contributes little to human survival. Researchers have thus wondered how and why cats came to live among people.

Experts have traditionally thought that the Egyptians were the first to domesticate the cat, some 3,600 years ago.

But recent genetic and archaeological discoveries indicate that cat domestication began in the Fertile Crescent, perhaps around 10,000 years ago, when agriculture was getting under way.

The findings suggest that cats started making themselves at home around people to take advantage of the mice and food scraps found in their settlements.

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THE ALOOF AND ELUSIVE NATURE OF CATS IS PERHAPS THEIR MOST DISTINCTIVE FEATURE, endearing to some and exasperating to others. Despite such mercurial tendencies, the house cat is the most popular pet in the world. A third of American households have feline members, and more than 600 million cats live among humans worldwide. Yet as familiar as these animals are, a complete understanding of their origins has proved elusive. Whereas other once wild animals were domesticated for their milk, meat, wool or labor, cats contribute virtually nothing in the way of sustenance or work. How, then, did they become fixtures in our homes?

Scholars long believed that the ancient Egyptians were the first to keep cats as pets, starting around 3,600 years ago. But genetic and archaeological discoveries made over the past 10 years have revised this scenario—and have generated fresh insights into both the ancestry of the domestic cat and how its relationship with humans evolved.

CAT'S CRADLE

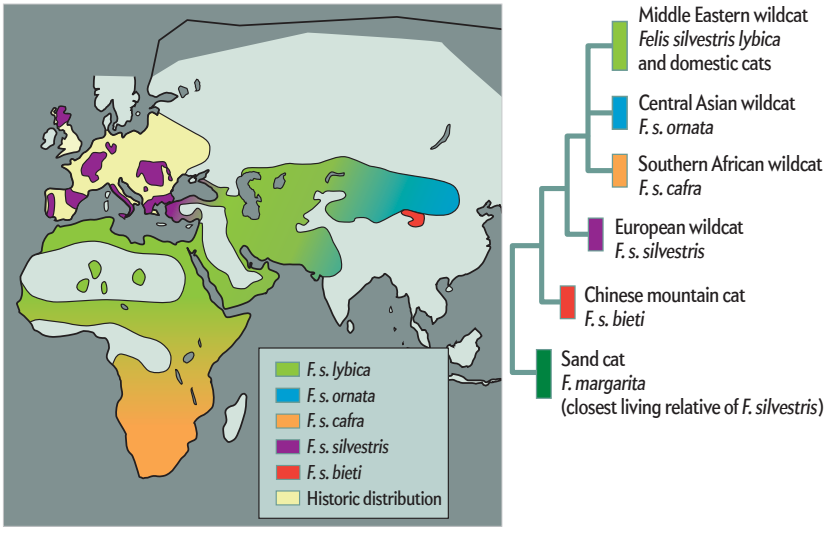
THE QUESTION of where domestic cats first arose has been challenging to resolve for several reasons. Although a number of investigators suspected that all varieties descend from just one cat species—*Felis silvestris,* the wildcat—they could not be certain. In addition, that species is represented by populations living throughout the Old World—from Scotland to South Africa and from Spain to Mongolia—and until recently scientists had no way of determining unequivocally which of these wildcat populations gave rise to the tamer, domestic kind. Indeed, as an alternative to the Egyptian origins hypothesis, some researchers had even proposed that cat domestication occurred in a number of different locations, with each domestication spawning a different breed. Confounding the issue was the fact that members of these wildcat groups are hard to tell apart from one another and from feral domesticated cats with so-called mackerel-tabby coats because all of them have the same pelage pattern of curved stripes and they interbreed freely with one another, further blurring population boundaries.

In 2000 one of us (Driscoll) set out to tackle the question by assembling DNA samples from some 979 wildcats and domestic cats in southern Africa, Azerbaijan, Kazakhstan, Mongolia and the Middle East. Because wildcats typically defend a single territory for life, he expected that the genetic composition of wildcat groups would vary across their geographical ranges but remain stable over time, as is observed in many other felid species.

FINDINGS

The House Cat's Ancestor

Researchers examined DNA belonging to nearly 1,000 wildcats and domestic cats from across the Old World to determine which subspecies of the wildcat, *Felis silvestris,* gave rise to the house cat. They found that the DNA clustered into five groups, based on similarity of sequence, and noted that the wildcats within each group came from the same region of the world (*map*). The domestic cats, however, grouped only with *F. silvestris lybica,* the Middle Eastern wildcat. This result established that all domestic cats are descended from *F. s. lybica* alone (*family tree*).



PRECEDING PAGES: JANE BURTON Getty Images

Illustration by Jen Christiansen

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If regional indigenous groups of these animals could be distinguished from one another on the basis of their DNA and if the DNA of domestic cats more closely resembled that of one of the wildcat populations, then he would have clear evidence for where domestication began.

In the genetic analysis, published in 2007, Driscoll, another of us (O'Brien) and their colleagues focused on two kinds of DNA that molecular biologists traditionally examine to differentiate subgroups of mammal species: DNA from mitochondria, which is inherited exclusively from the mother, and short, repetitive sequences of nuclear DNA known as microsatellites. Using established computer routines, they assessed the ancestry of each of the 979 individuals sampled based on their genetic signatures. Specifically, they measured how similar each cat's DNA was to that of all the other cats and grouped the animals having similar DNA together. They then asked whether most of the animals in a group lived in the same region.

The results revealed five genetic clusters, or lineages, of wildcats. Four of these lineages corresponded neatly with four of the known subspecies of wildcat and dwelled in specific places: *F. silvestris silvestris* in Europe, *F. s. bieti* in China, *F. s. ornata* in Central Asia and *F. s. cafra* in southern Africa. The fifth lineage, however, included not only the fifth known subspecies of wildcat—*F. s. lybica* in the Middle East—but also the hundreds of domestic cats that were sampled, including purebred and mixed-breed felines from the U.S., the U.K. and Japan. In fact, genetically, *F. s. lybica* wildcats collected in remote deserts of Israel, the United Arab Emirates and Saudi Arabia were virtually indistinguishable from domestic cats. That the domestic cats grouped with *F. s. lybica* alone among wildcats meant that domestic cats arose in a single broad locale, the Middle East, and not in other places where wildcats are native.

Once we had figured out where domestic cats came from, the next step was to ascertain when they had become domesticated. Geneticists can often estimate when a particular evolutionary event occurred by studying the quantity of random genetic mutations that accumulate at a steady rate over time. But this so-called molecular clock ticks a mite too slowly to precisely date events as recent as the past 10,000 years, the likely interval for cat domestication. To get a bead on when the taming of the cat began, we turned to the archaeological record. One find has proved especially informative in this regard.

In 2004 Jean-Denis Vigne of the National Museum of Natural History in Paris and his colleagues reported unearthing the earliest evidence suggestive of humans keeping cats as pets. The discovery comes from the Mediterranean island of Cyprus, where 9,500 years ago an adult human of unknown gender was laid to rest in a shallow grave. An assortment of items accompanied the body—stone tools, a lump of iron oxide, a handful of seashells and, in its own tiny grave just 40 centimeters away, an eight-month-old cat, its body oriented in the same westward direction as the human's.

Because wildcats are not native to Mediterranean islands other than Sicily, we know that people must have brought them over by boat, probably from the adjacent Levantine coast. Together the transport of cats to the island and the burial of the human with a cat indicate that people had formed special, intentional relationships with cats nearly 10,000 years ago in some parts of the Middle East. This locale is consistent with the geographical origin we arrived at through our genetic analyses. It appears, then, that cats were being tamed just as humankind was establishing the first settlements in a part of the Middle East known as the Fertile Crescent—the Cradle of Civilization.

FOSSIL DISCOVERY

Early Domestication

Traditionally the ancient Egyptians have been credited with domesticating the cat by roughly 3,600 years ago. But in 2004 archaeologists working on the Mediterranean island of Cyprus discovered a 9,500-year-old burial of an adult human and a cat (*circled on photograph at left and on map at right*). Because cats are not native to Cyprus, people must have brought them over by boat, probably from the nearby Levantine coast. The find thus suggests that people in some parts of the Middle East began keeping cats as pets long before the Egyptians did.

FROM "EARLY TAMING OF THE CAT IN CYPRUS," BY J.-D. VIGNE, J. GUILAINE, K. DEBUE, L. HAYE AND P. GERARD, IN *SCIENCE*, VOL. 304; APRIL 2004

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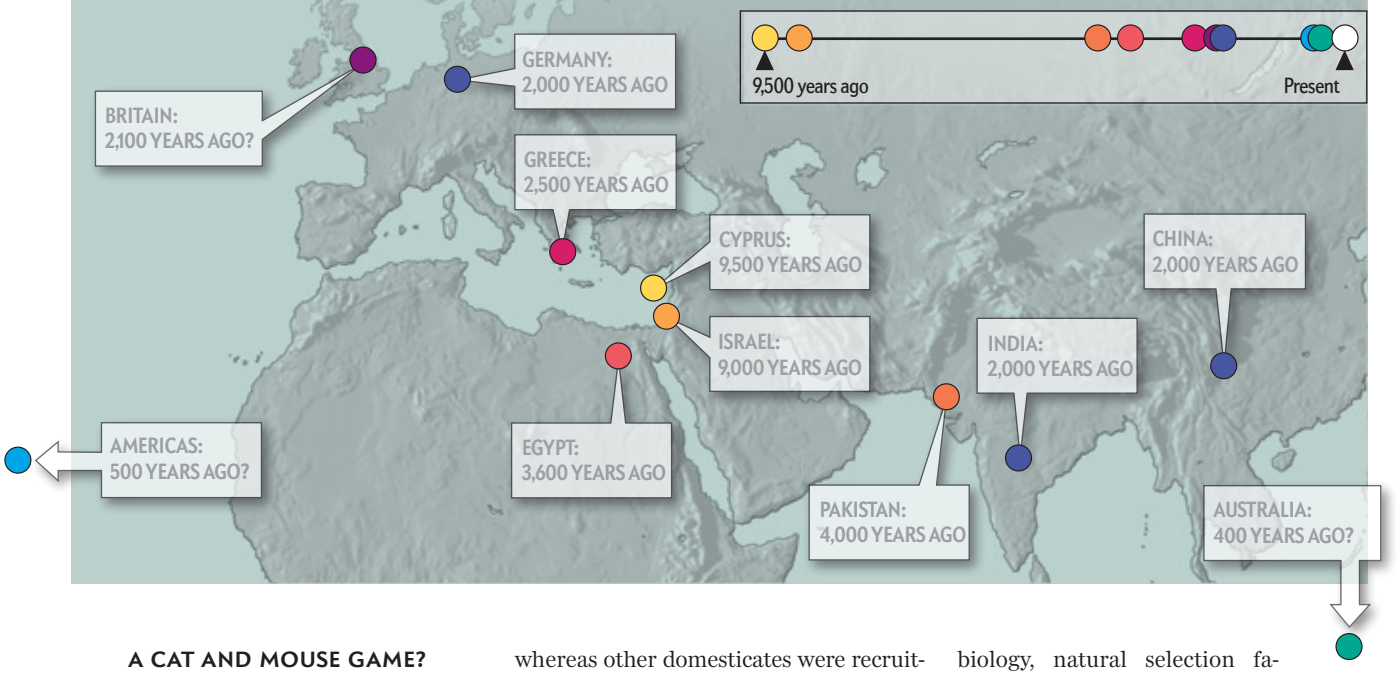
DISPERSAL

Have Cats, Will Travel

As agriculture and permanent human settlements spread from the Fertile Crescent to the rest of the world, so, too, did domestic cats. The map below shows the earliest putative occurrences of domestic cats in regions around the globe.



A CAT AND MOUSE GAME?

WITH THE GEOGRAPHY and an approximate age of the initial phases of cat domestication established, we could begin to revisit the old question of why cats and human beings ever developed a special relationship. Felids in general are unlikely candidates for domestication. The ancestors of most domesticated animals lived in herds or packs with clear dominance hierarchies. (Humans unwittingly took advantage of this structure by supplanting the alpha individual, thus facilitating control of entire cohesive groups.) These herd animals were already accustomed to living cheek by jowl, so provided that food and shelter were plentiful, they adapted easily to confinement.

Felids, in contrast, are solitary hunters that defend their home ranges fiercely from others of the same sex (the pride-living lions are the exception to this rule). Moreover, whereas most domesticates feed on widely available plant foods, felids are obligate carnivores, meaning they have a limited ability to digest anything but meat—a far rarer menu item. In fact, they have lost the ability to taste sweet carbohydrates altogether. And as to utility to humans, let us just say that our cats do not take instruction well. Such attributes suggest that whereas other domesticates were recruited from the wild by humans who bred them for specific tasks, ancestors of domestic cats most likely chose to live among humans because of opportunities they found for themselves.

Early settlements in the Fertile Crescent between 9,000 and 10,000 years ago, during the Neolithic period, created a completely new environment for any wild animals that were sufficiently flexible and inquisitive (or scared and hungry) to exploit it. The house mouse, *Mus musculus domesticus,* was one such animal. Archaeologists have found remains of this rodent, which originated in the Indian subcontinent, among the first human stores of wild grain from Israel, which date to around 10,000 years ago. The house mice could not compete well with the local wild mice outside, but by moving into people's homes and silos, they thrived.

It is almost certainly the case that these house mice attracted cats. But the trash heaps on the outskirts of town were probably just as great a draw, providing year-round pickings for those felines resourceful enough to seek them out. Both these food sources would have encouraged wildcats to adapt to living with people; in the lingo of evolutionary biology, natural selection favored those wildcats that were able to cohabit with humans and thereby gain access to the trash and mice.

Over time, wildcats more tolerant of living in human-dominated environments began to proliferate in villages throughout the Fertile Crescent. Natural selection in this new niche would have been principally for tameness, but competition among cats would also have continued to influence their evolution and limit how pliant they became. Because these proto–domestic cats were undoubtedly mostly left to fend for themselves, their hunting and scavenging skills remained sharp. Even today most domesticated cats are free agents that can easily survive independently of humans, as evinced by the plethora of feral cats around the world.

Considering that small cats do little obvious harm, people probably did not mind their company. They might have even encouraged the cats to stick around when they saw them dispatching mice and snakes. Cats may have held other appeal, too. Some experts speculate that wildcats just so happened to possess features that might have preadapted them to developing a relationship with people. In particular, these cats have "cute" features—large eyes, a snub face and a high,

Map by Jen Christiansen

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round forehead, among others—that are known to elicit nurturing from humans. In all likelihood, then, some people took kittens home simply because they found them adorable, giving cats a singular foothold at the human hearth.

Why was *F. s. lybica* the only subspecies of wildcat to be domesticated? Anecdotal evidence suggests that certain other subspecies, such as the European wildcat and the Chinese mountain cat, are less tolerant of people. If so, this trait alone could have precluded their adoption into homes. The friendlier southern African and Central Asian wildcats, on the other hand, might very well have become domesticated under the right conditions. But *F. s. lybica* had the good luck of proximity to the first human settlements. As agriculture spread out from the Fertile Crescent, so, too, did the tame scions of *F. s. lybica,* filling the same niche in each region they entered—and effectively shutting the door on local wildcat populations. Had domestic cats from the Fertile Crescent never arrived in Africa or Asia, perhaps the indigenous wildcats in those regions would have been drawn to homes and villages as urban civilizations developed there.

RISE OF THE GODDESS

WE DO NOT KNOW how long it took to transform the Middle Eastern wildcat into an affectionate home companion. Animals can be domesticated rapidly under controlled conditions. But without doors or windowpanes, Neolithic farmers would have been hard-pressed to control the breeding of cats even if they wanted to. It seems reasonable to suggest that the lack of human influence on breeding and the probable intermixing of proto–domestic cats and wildcats militated against rapid taming, causing the metamorphosis to occur over thousands of years.

Although the exact timeline of cat domestication remains uncertain, long-known archaeological evidence affords some insight into the process. After the Cypriot find, the next oldest hints of an association between humans and cats are a feline molar tooth from an archaeological deposit in Israel dating to roughly 9,000 years ago and another tooth from Pakistan dating to around 4,000 years ago.

Testament to full domestication comes from a much later period. An ivory cat statuette from Israel, more than 3,200

TIMELINE

From Wild to Mild

Researchers believe, based on archaeological and historical records, that the transformation of the Middle Eastern wildcat into a ubiquitous pet transpired over thousands of years.

1 **10,500–9,500 years ago** House mouse remains preserved with human stores of grain in Israel; origin of agriculture and of permanent human settlements creates opportunities for cats willing to get close enough to humans to hunt house mice

9,500 years ago Human and cat double burial on Mediterranean island of Cyprus; earliest evidence of special relationship between people and cats

3,600 years ago Artists paint domesticated cats from Thebes, Egypt; oldest clear evidence of fully domesticated cat

2 **3,200–3,400 years ago** Ivory cat statuette sculpted in Israel; suggests cats were a common sight around human settlements in the Fertile Crescent

3 **2,900 years ago** Cats become "official deity" of Egypt in the form of the goddess Bastet; huge number of cats sacrificed and mummified in her sacred city indicates that Egyptians were breeding domestic cats

2,300 years ago The height of cat worship in Egypt; the Ptolemaic rulers maintain strict bans on the export of cats

2,000 years ago Cat remains preserved at the German site of Tofting in Schleswig; increasing references to cats in art and literature show that domestic cats were common throughout Europe

4 **1350–1767** The Tamara Maew (or "Cat-Book Poems"), composed by Buddhist monks in Thailand, describes indigenous natural breeds, such as the Siamese, which arose largely through genetic drift, as opposed to human intervention

1800s Most of the modern breeds developed in the British Isles, according to writings of English natural history artist Harrison Weir

1871 Cat show at the Crystal Palace in London is first to include human-created breeds

5 **2015** Breeders have created more than 60,000 Bengal cats, hybrids of domestic and Asian leopard cats

1

2

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4

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STEPHEN DALTON *Science Source* (1); DAVID HARRIS *Israel Museum, Jerusalem* (2); GETTY IMAGES (3, 4, 5)

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years old, suggests the cat was a common sight around homes and villages in the Fertile Crescent before its introduction to Egypt. This scenario makes sense, given that all the other domestic animals (except the donkey) and plants were introduced to the Nile Valley from the Fertile Crescent. But it is Egyptian paintings from the so-called New Kingdom period—Egypt's golden era, which began nearly 3,600 years ago—that provide the oldest known unmistakable depictions of full domestication. These paintings typically show cats poised under chairs, sometimes collared or tethered, and often eating from bowls or feeding on scraps. The abundance of these illustrations signifies that cats had become common members of Egyptian households by this time.

It is in large part as a result of evocative images such as these that scholars traditionally perceived ancient Egypt as the locus of cat domestication. Still, even the oldest Egyptian representations of wildcats are 5,000 to 6,000 years younger than the 9,500-year-old Cypriot burial. Although ancient Egyptian culture cannot claim initial domestication of the cat among its many achievements, it surely played a pivotal role in subsequently molding the dynamic of domestication and the spread of cats throughout the world. Indeed, the Egyptians took the love of cats to a whole new level. By 2,900 years ago the domestic cat had become the official deity of Egypt in the form of the goddess Bastet, and such cats were sacrificed, mummified and buried in great numbers at Bastet's sacred city, Bubastis. The sheer number of cat mummies found there, measured by the ton, indicates that Egyptians were not just harvesting feral or wild populations but, for the first time in history, were actively breeding domestic cats.

Egypt officially prohibited the export of its venerated cats for centuries. Nevertheless, by 2,500 years ago the animals had made their way to Greece, proving the inefficacy of export bans. By 2,000 years ago grain ships sailed directly from Alexandria to destinations throughout the Roman Empire, and cats are certain to have been onboard to keep the rats in check. Thus introduced, cats would have established colonies in port cities and then fanned out from there. Later, when the Romans expanded their empire, domestic cats traveled with them and became common throughout Europe. Evidence for their spread comes from the German site of Tofting in Schleswig, which dates to between the fourth and 10th centuries, as well as increasing references to cats in art and literature from that period. (Oddly, domestic cats seem to have reached the British Isles before the Romans brought them over—a dispersal that researchers cannot yet explain.)

Meanwhile, on the opposite side of the globe, domestic cats had presumably spread to the Orient almost 2,000 years ago, along well-established trade routes between Greece and Rome and the Far East, reaching China by way of Mesopotamia and arriving in India via land and sea. Then something interesting happened. Because no native wildcats with which the newcomers could interbreed lived in the Far East, the Oriental domestic cats soon began evolving along their own trajectory. Small, isolated groups of Oriental domestics gradually acquired distinctive coat colors and other mutations through a process known as genetic drift, in which traits that are neither beneficial nor maladaptive become fixed in a population.

This drift led to the emergence of the Korat, the Siamese, the Birman and other "natural breeds," which were described by Thai Buddhist monks in a book called the Tamara Maew (meaning "Cat-Book Poems") that may date back to 1350. The putative antiquity of these breeds received support from the results of genetic studies announced in 2008, in which Marilyn Menotti-Raymond of the National Cancer Institute and Leslie Lyons, now at the University of Missouri, found DNA differ-

GANDEE VASAN Getty Images (cats); TIM FLACH Getty Images (dogs)

BREEDING

The Truth about Cats and Dogs

Unlike dogs, which exhibit a huge range of sizes, shapes and temperaments, house cats are relatively homogeneous, differing mostly in the characteristics of their coats. The reason for the relative lack of variability in cats is simple: humans have long bred dogs to assist with particular tasks, such as hunting or sled pulling, but cats, which lack any inclination for performing most tasks that would be useful to humans, experienced no such selective breeding pressures.

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ences between today's European and Oriental domestic cat breeds indicative of more than 700 years of independent cat breeding in Asia and Europe.

As to when domestic cats reached the Americas, little is known. Christopher Columbus and other seafarers of his day reportedly carried cats with them on transatlantic voyages. And voyagers onboard the *Mayflower* and residents of Jamestown are said to have brought cats with them to control vermin and to bring good luck. How house cats got to Australia is even murkier, although recent DNA analysis by our team affirms that the Australian cats are of a European type (rather than Oriental) and likely arrived with European explorers in the 1600s, 40,000 years after the aboriginal Australians settled the continent.

BREEDING FOR BEAUTY

ALTHOUGH HUMANS might have played some minor role in the development of the natural breeds in the Orient, concerted efforts to produce novel breeds did not begin until relatively recently. Even the Egyptians, who we know were breeding cats extensively, do not seem to have been selecting for visible traits, probably because distinctive variants had not yet arisen: in their paintings, both wildcats and house cats are depicted as having the same mackerel-tabby coat. Experts believe that most of the modern breeds were developed in the British Isles in the 19th century, based on the writings of English natural history artist Harrison Weir. And in 1871 the first proper fancy cat breeds—breeds created by humans to achieve a particular appearance—were displayed at a cat show held at the Crystal Palace in London (a Persian won, although the Siamese was a sensation).

Today the Cat Fancier's Association and the International Cat Association recognize nearly 60 breeds of domestic cat. Just a dozen or so genes account for the differences in coat color, fur length and texture, as well as other, subtler coat characteristics, such as shading and shimmer, among these breeds.

Thanks to the sequencing of the entire genome of an Abyssinian cat named Cinnamon in 2007, geneticists have identified the mutations that produce such traits as tabby patterning, black, white and orange coloring, long hair and many others. Beyond differences in the pelage-related genes, however, the genetic variation between domestic cat breeds is very slight—comparable to that seen between adjacent human populations, such as the French and the Italians.

The wide range of sizes, shapes and temperaments seen in dogs—consider the Chihuahua and Great Dane—is absent in cats. Felines show much less variety because, unlike dogs—which were bred from prehistoric times for such tasks as guarding, hunting and herding—early cats were under no such selective breeding pressures. To enter our homes, they had only to evolve a people-friendly disposition.

So are today's house cats truly domesticated? Well, yes, certainly they are—but perhaps only just. Although they satisfy the criterion of tolerating people, most domestic cats are feral and do not rely on people to feed them or to find them mates. And whereas other domesticates, like dogs, look quite distinct from their wild ancestors, the average domestic cat largely retains the wild body plan. It does exhibit a few morphological differences, however—namely slightly shorter legs, a smaller brain and, as Charles Darwin noted, a longer intestine, which may have been an adaptation to scavenging kitchen scraps.

The house cat has not stopped evolving, though—far from it. Armed with artificial insemination and in vitro fertilization technology, cat breeders today are pushing domestic cat genetics into uncharted territory: they are hybridizing house cats with other felid species to create exotic new breeds. The Bengal and the Caracat, for example, resulted from crossing the house cat with the Asian leopard cat and the caracal, respectively. The domestic cat may thus be on the verge of an unprecedented and radical evolution into a multispecies composite whose future can only be imagined. SA

GENETICS

Saving the Scottish Wildcat

As the northernmost representative of the European wildcat, the Scottish wildcat lives under environmental and climatic conditions unlike those experienced by any other wildcat. It is also critically endangered, thanks to interbreeding with feral domestic cats. According to the latest rough estimate, perhaps only 400 pure Scottish wildcats survive. But sorting the Scottish feline from hybrids and domestic cats is challenging because they all look so similar. To that end, the authors recently discovered a unique genetic signature of the Scottish wildcat that permits precise identification. This development will facilitate implementation of legal protection of this animal.

Carlos A. Driscoll is WWF Chair of Conservation Genetics at the Wildlife Institute of India. In 2007 he published the first DNA-based family tree of *Felis silvestris,* the species to which the domestic cat belongs. He is currently hunting for the individual genes that determine domestic behavior. **Juliet Clutton-Brock**, a founding member of the International Council for Archaeozoology, is a pioneer in the study of domestication and the early interface between the wild and the domestic. **Andrew C. Kitchener** is principal curator of vertebrates at National Museums Scotland, where he studies geographical variation and hybridization in mammals and birds. **Stephen J. O'Brien** was chief of the National Cancer Institute's Laboratory of Genomic Diversity until 2012 and is now chief scientific officer at the Dobzhansky Center for Genome Bioinformatics at St. Petersburg State University in Russia. He has studied the genetics of cheetahs, giant pandas, pumas and whales and of human infection by HIV.

MORE TO EXPLORE

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The Inner life of Cats

If you have ever wondered why your cat behaves the way it does, wonder no more

Illustrations by Mark Allen Miller

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ASK ME ANOTHER

As anyone who has spent time with cats knows, our feline companions are mysterious—much more so than those *other* furry family members. Here John Bradshaw, author of *Cat Sense* (Basic Books, 2013), fields a selection of questions submitted by *Scientific American* editors and Twitter followers about the cat's many quirks. Bradshaw is a visiting fellow at the University of Bristol School of Veterinary Sciences in England, where he studies the behavior and welfare of cats and dogs, as well as their interactions with people.

Interview by Kate Wong

Are cats less domesticated than dogs? Are they becoming more domesticated over time? Cats are far more similar to their wild ancestors than dogs are to wolves, so dogs are in that sense the more domesticated of the two species. As they adapted to living alongside humans, cats became more sociable with one another and much more accepting of people, but there is no evidence that they have changed much more than that over the past few thousand years.

Will cats, which require meat, eventually evolve to eat a broader array of foods as dogs do? Cats and dogs belong to a group of mammals known as Carnivora, and the wild ancestors of both species dined primarily on meat. Recent DNA analyses indicate that over the course of their evolution, dogs have acquired more copies of the so-called amylase gene, which makes an enzyme that helps to break down starch. Having more copies of this gene has allowed dogs to eat a more omnivorous diet. In contrast, the cat family, known as Felidae, lost the genes that encode several key enzymes—including those that manufacture vitamin A, prostaglandins and the amino acid taurine—early in its evolution. Whereas dogs (and humans) can synthesize these substances from plant-based precursors, cats have to obtain them from meat. To expand their diet, cats would have to evolve physiological traits that allow them to synthesize these and other key nutrients from plant foods. This capacity has not emerged during the 10 million years of felid evolution, so it seems unlikely to arise spontaneously in our domestic cats.

Why do cats purr? Cats purr because they have something to say, which roughly translated is "please keep still and pay attention to me." Kittens purr to persuade their mothers to keep on nursing them, and pet cats purr when they want to be stroked. The vibrations emanating from the purr certainly have a calming effect on people. Yet sick cats will also purr as a cry for help. So purring doesn't always mean "I'm happy." Some research-

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ers have claimed that the vibrations from purring might help heal bone damage in an injured cat.

How do they purr? The purr is an unusual vocalization, made by rattling the vocal cords together rather than vibrating them by pushing air past them, which is how cats—and humans—generate all their other vocal sounds. That's why cats can purr when they're breathing in and breathing out. Most species of wildcats can purr, including the cheetah. The exceptions are the big cats—lion, tiger, jaguar and leopard—whose voice boxes are modified so that they can roar.

Why do house cats have so many vocalizations compared with wildcats? House cats are much noisier than feral cats, although they have fewer vocalizations than some other species. The jungle cat from Asia, for example, has a couple more that are not in the house cat's repertoire, namely the "ow" and the "gurgle." The house cat's characteristic sound, the meow, is hardly ever heard in feral cat colonies, except occasionally when mother cats are communicating with their kittens. Feral cats diligently monitor one another's comings and goings, so they don't need to announce their presence vocally. Cats that live with humans, however, learn that meowing is a good way of getting our attention: our pet felines often find that we have our noses buried in a book or a screen, so they meow to get us to acknowledge them. Some pets develop a "private language" of meows that only their owners understand, each signifying something different that the cat needs. Also, certain breeds are notoriously chatty, the Siamese in particular.

Do cats think of their owners as parents? Siblings? Friends? By rubbing around our legs when they greet us, cats show that they regard us as friendly but at the same time slightly superior to them. When living in a family group, kittens rub on their mothers, females rub on males and smaller cats rub on bigger cats. The reverse rarely occurs—an indicator of the small imbalance of power in each of these relationships.

How can you get a cat to love you? Cats naturally feel affection for those who feed, look after and play with them, although they don't always make that obvious. Trust can be harder to win because some cats are just nervous. One trick is to always allow the cat to approach you rather than forcing yourself on the cat when you feel like it. When the cat does approach, reward it with a few treats and let it leave as soon as it wants to. You should find that it comes to you a little sooner, and stays for a little longer, each time.

Why do cats sometimes suddenly bite or scratch the person who is petting them? You have probably missed the warning signs that the cat has had enough. Some cats, even if they enjoy being petted, also tire of it very quickly. Flattened ears and a slight twitching of the tail can signal that they have had their fill. If you have such a cat, try breaking off from stroking it every few seconds and allow it to move away if it wants to.

Can cats get jealous? Research has demonstrated that dogs can get jealous, so cats probably can, too. For both species jealousy is an in-the-moment emotion they experience when they see that another individual is getting the attention they are craving: they don't remember being jealous once the moment has passed. As with dogs, cats have a limited concept of time: they can learn to distinguish between different time intervals but only when these intervals are limited to a few seconds. Thinking back into the more distant past is probably beyond their abilities.

CATS HAVE TO EAT MEAT BECAUSE DURING THE EVOLUTION OF THE CAT FAMILY, MANY MILLIONS OF YEARS AGO, THEIR COMMON ANCESTOR LOST CERTAIN KEY ENZYMES THAT ALLOW MORE OMNIVOROUS CARNIVORES, SUCH AS DOGS, TO PROCESS PLANT-BASED FOODS.

Do cats remember different people or just the people they see on a daily basis? Scientists have not studied this specific trait directly, but cats do seem to forget other cats once they have been separated for a long time, so the same probably applies to people as well. Dogs, for whom humans are much more important, can remember people by their scent for months, probably years.

Do coat colors and patterns correspond to certain personality traits in cats? Cat owners commonly believe that coat color can predict the personality of their pet, but there's no evidence that this is universally true. Locally, a very successful male can produce a lot of kittens that both look like him and behave like him because of their shared genes, which might explain how people have come to associate coat color with personality. Among pedigree cats, the major breed types do have characteristic personalities: the so-called oriental breeds tend to be particularly active, the exotics more laid-back. Cats that are hybrids of domesticated cats and wildcats exhibit even stronger breed-specific personality traits. For example, Bengals, which are a cross between domestic cats and the Asian leopard cat, tend to be extremely adventurous and sleep for only about half the time that a typical domestic cat does.

Why do cats bring their kills to their humans? It is tempting to see these kills as presents from our feline companions, but they are not intended that way. Cats take their kills somewhere safe before they eat them. If this location happens to be in or near the kitchen, they are automatically reminded that commercial cat food is much tastier than mouse,

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and hence they abandon their catch then and there.

Why do they knock objects off tables and shelves? Some cats are just clumsier than others, and material possessions mean nothing to them. Others will bat items over the edge simply to get their owner's attention. Sometimes they seem to do it for their own entertainment or because they have learned that this is a game that their owner seems to enjoy.

Do indoor cats suffer from not being able to go outside? If a cat has lived indoors all its life, it probably doesn't "miss" what it has never experienced. Outdoor cats that are suddenly confined do get stressed, however. All indoor cats should be given plenty of stimulation—hunting games using preylike toys are ideal.

Why do cats sometimes suddenly decide to run around like crazy for no apparent reason? Cats can get quite frustrated if they are bored or if they are stressed, perhaps because they have just seen a rival cat through the window. Under such circumstances, the slightest movement, perhaps just a speck of dust caught in a shaft of light, can set them off. Regular play sessions can help dissipate all that energy and relieve any stress.

Why do cats love to climb into boxes, including ones that seem too small? Cats like to feel well protected, especially when they intend to sleep, and cardboard cartons can be ideal for a secure nap. Why some seem to prefer too small boxes over just right ones is a mystery, though.

Why do cats climb to heights that they are subsequently afraid to jump down from? Because cats' claws face backward, they're much more useful for running up trees than for climbing down. (The margay, a tree-dwelling South American cat, has double-jointed ankles and wrists that allow it to descend as easily as it ascends.) Inexperienced or frightened cats may go higher than they should. But they usually succeed in descending eventually because they have a reflex that enables them to fall safely, even from quite considerable heights. They stretch all four legs out sideways, so

CITIZEN SCIENCE

Be a Cat Researcher

Cat lovers around the globe can help researchers better understand the feline mind while helping cats lead happier and healthier lives. The following citizen science projects will be active through 2015. In some cases, you do not need to live with a cat to participate.

Track Your Cat

Your Wild Life and the North Carolina Museum of Natural Sciences
http://cats.yourwildlife.org
Live with a cat that goes outside? Investigators know very little about where cats go when they leave the home and even less about why some travel the open road and others stay nearby. In this project, set up a GPS cat-tracking device and find out where your cat goes.

Cat Tracking Down Under

Discovery Circle, University of South Australia
www.discoverycircle.org.au/projects/cat-tracker
Do cats around the world show similar movement patterns? Does the local environment affect how cats roam? This cat-tracking project in South Australia—open to anyone in the region, not just cat owners—will provide a cross-continental comparison of cat behavior. It includes GPS cat tracking, a cat personality test and a general survey.

Genetic and Genomic Resources for Cats

Cornell Feline Health Center, Cornell University College of Veterinary Medicine
www.vet.cornell.edu/FHC/health_discovery/FelineBiobank.cfm
What role do genes play in common feline diseases? By comparing DNA from healthy cats with DNA from cats with one or more common diseases, scientists can better understand the role that genes may play in these conditions. This project could assist veterinarians in their ability to diagnose and treat common diseases. The project is looking for DNA samples from healthy cats more than 10 years old.

New Anticancer Drugs for Mammary Cancer in Cats

Cornell Feline Health Center, Cornell University College of Veterinary Medicine
www.vet.cornell.edu/FHC/health_discovery/Mammaryglandstudy.cfm
Is there a way to stop mammary cancer in its tracks? Help reveal how feline mammary cancer develops and lay the groundwork for new ways to treat it. Investigators are accepting both normal and cancerous feline mammary gland tissue samples from female cats.

Understanding Cat Pain

University of Lincoln, England
http://ucpproject.co.uk
Pain is an unpleasant sensory and emotional experience that involves a physical response as well as behavioral change. This project explores the facial, postural and vocal expressions of pain in cats—information that gives owners and veterinarians a leg up on recognizing this emotion earlier so cats can be treated before their welfare is compromised. If you own a cat that you think is in pain, contribute a video or picture. You can also take a quick quiz and check your ability to detect pain in these animals.

—Julie Hecht

Julie Hecht is a Ph.D. student studying dog behavior and author of the Dog Spies blog at ScientificAmerican.com

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CATNIP'S MAGIC

HAVE YOU WONDERED WHY SOME CATS EXHIBIT STRANGE behavior when exposed to catnip? They act much like a female cat in heat: They may rub their head and body on the herb or jump, roll around, vocalize and salivate. This response lasts for about 10 minutes, after which the cat becomes refractory to catnip's effects for roughly 30 minutes. Response to catnip is hereditary; about 70 percent of cats exhibit this behavior in the plant's presence, although it does not affect kittens until they are about six months old and begin to reach sexual maturity.

The genetically susceptible cats are responding to a volatile oil in the stems and leaves of the plant *Nepeta cataria* and other *Nepeta* species, which are members of the mint family. When the oil, named nepetalactone, enters the cat's nasal tissue, it apparently binds to proteins that stimulate sensory neurons. These nerve cells, in turn, provoke a response in neurons in the brain's olfactory bulb, which project to several regions of the brain, including the amygdala (two neuronal clusters deep in the temporal lobes that mediate emotional responses to stimuli) and the hypothalamus (the brain's "master gland"), which is known to play a role in regulating everything from hunger to emotions.

The hypothalamus, acting through the pituitary gland, alters hormonal levels to spur the sexual-like response. In other words, the cat essentially responds to the oil as if it were a pheromone emitted by another cat. Catnip is considered to be nonaddictive and completely harmless to cats.

—Ramona Turner

Ramona Turner is a veterinarian practicing in Fresno, Calif.

that the loose skin on their belly forms a kind of parachute. Then, a split second before reaching the ground, they push their feet downward and arch their back to minimize the shock of landing.

Why do some cats go crazy for catnip and others show no response at all? The catnip response is a bit of an enigma because it consists of seemingly random segments of play (pouncing, clutching with the claws), socializing (cheek rubbing) and female sexual behavior (rolling onto the back, for example). Many cat species have this reaction to the herb, including lion, tiger, leopard and lynx. Yet not all individuals in these species show the response because it is controlled by a single gene that only about two thirds of cats carry [see "Catnip's Magic," above]. There is no evidence to suggest that cats that ignore catnip are deficient where play, socializing and sex are concerned, however. The catnip response may simply be an evolutionary accident.

Why do cats lick and chew plastic bags, power cords and other nonfood items? Veterinarians have noted an unhealthy taste for plastics in some cats but have never convincingly explained it. Cats may be trying to alleviate stress. Among oriental cat breeds, adults commonly suck, chew and eat fabrics, especially wool, in response to stress. Also, kittens of all kinds that are weaned too early may develop the habit of suckling on a blanket, usually purring and kneading with their front paws at the same time, as if the blanket were their mother.

Why do they chew their fur? There are two possible reasons for this behavior. One is itchy skin, possibly caused by fleas or other parasites, or an allergy. But persistent overgrooming on one spot or pulling out clumps of fur can also be signs of chronic stress, perhaps because of conflict with another cat in the house or in the neighborhood.

Why do cat feet sometimes smell like tortilla chips? A common minor fungal skin infection, similar to athlete's foot in humans, often produces this smell. Dogs may carry this fungus, too.

Why can't domestic cats go without food for long, like their big cat cousins can? They get fatty liver disease in a couple of days. All cats, big and small, can suffer from fatty liver disease, in which fat released from other parts of the body accumulates in the liver, blocking its ability to carry out key functions such as recycling red blood cells. This condition can occur as a result of cancer, diabetes or kidney disease, but it can also be triggered by the cat not eating for some reason (stress is a common cause in pet cats). It comes on much more quickly in obese cats, so it's probably less common in big cat species simply because living in the wild they're unlikely to be overweight.

Why are cats so finicky about food and their litter boxes? Why are they so sensitive to any change in routine? Cats have much more exacting nutritional requirements than dogs do, so they have to be careful about what they eat. Also, as solitary hunters, their ancestors could afford to eat in their own good time. Dogs, in contrast, are descended from pack-hunting wolves, which evolved to eat quickly so they could grab their share of the kill. Cats also prefer to hide their feces, which would otherwise betray their whereabouts to prey and predators alike, hence their reluctance to use a dirty litter box. Cats are much more sensitive than dogs are to any change in their environment because they are territorial animals that get their sense of security from the place where they live. That's why cats often try to get back to their owners' previous home in the first few weeks following a house move.

Will cats really consume their deceased owners in some situations? If they are literally dying of hunger, cats (and dogs) will eat anything available. I'm sure that they don't mean to cause offense!

Kate Wong is a cat lover and a senior editor at *Scientific American*.

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WHY CATS TASTE NO SWEETS

SUGAR AND SPICE AND EVERYTHING nice hold no interest for a cat. Our feline friends are interested in only one food: meat. This predilection is not solely the result of an inner killer just waiting to catch a bird or torture a mouse. It also occurs because cats lack the ability to taste sweetness.

The cause has been traced to a gene. The tongues of most mammals hold taste receptors—proteins on the cellular surface that bind to an incoming substance, activating the cell's internal workings and leading to a signal being sent to the brain. Humans enjoy at least five kinds of taste buds: sour, bitter, salty, umami (or meatiness) and sweet (as well as possibly fat). The sweet receptor is actually made up of two coupled proteins generated by two separate genes: *Tas1r2* and *Tas1r3*.

All cats, however—including lions, tigers and British longhairs, oh my!—lack a chunk of DNA that occurs in the *Tas1r2* gene of other mammals. As a result, the depleted feline gene (more properly called a pseudogene) does not code for the proper protein and thereby prevents cats from tasting sweets. "They don't taste sweet the way we do," says neurobiologist Joe Brand, former associate director and now member emeritus of the Monell Chemical Senses Center in Philadelphia.

Brand and his colleague Xia Li discovered the pseudogene about 12 years ago, when they followed up on decades of anecdotal evidence of cats' being sweetness-impaired, such as cats showing no preference for sweetened over regular water.

Of course, there are also plenty of anecdotal accounts pointing in the other direction: cats that eat ice cream, relish cotton candy or chase marshmallows. "Maybe some cats can use their [*Tas1r3* receptor] to taste high concentrations of sugar," Brand says. "Or perhaps they are cuing on some other compound that we cannot appreciate."

Scientists do know, however, that cats can taste things we cannot, such as adenosine triphosphate (ATP), the compound that supplies the energy in every living cell. "There isn't a lot hanging around in meat, but it's a signal for meat," Brand says. Plenty of other animals have a different array of receptors, Li says, from chickens that also lack the sweet gene to catfish that can detect amino acids in water at nanomolar concentrations. "Their receptor is more sensitive than the background concentration," Brand notes. "The catfish that detects the rotting food first is the one that survives."

Cats are not alone. Brand and his colleagues have since found that all felines (some 36 species) and several other species of strictly meat-eating mammals all lack a sweet receptor. Cats may also lack other components of the ability to enjoy (and digest) sugars, such as glucokinase in their liver—a key enzyme that controls the metabolism of carbohydrates and prevents glucose from flooding the animal's bloodstream.

Despite the cat's inability to handle sugar, most major pet food manufacturers use rice or other grains in their meals. "This may be why cats are getting diabetes," Brand offers. "Cat food today has up to 20 percent carbohydrates. Cats are not used to that—they can't handle it." What these fearsome predators of suburbia cannot taste may be hurting them. But it also means that most cat lovers don't have to worry about Kitty snatching their unattended dessert. —*David Biello*

David Biello is an associate editor at *Scientific American*.

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THE MYSTERY OF THE INNER EYELID

Cat's third eyelid

A CAT HAS UPPER AND LOWER EYELIDS THAT MEET WHEN the eye closes, along with a mysterious third eyelid—more properly called the *palpebra tertia,* also known as the nictitating membrane or "haw." Tucked in the inner corner of the cat's eye, the third eyelid is a biological curiosity long thought to be irrelevant, much like the human appendix or wisdom teeth. Veterinary articles written in the early 1900s even described methods for removing the extra eyelid to make it easier to examine the eye. But the third eyelid actually plays an important role in maintaining the eye's health. In fact, most mammals and birds have a third eyelid—those lacking one, such as humans and some of our fellow primates, are the true oddities.

The anatomy of the third eyelid is complex. It is a fold of tissue covered by a double-sided mucous membrane, the conjunctiva, which faces the inner surface of the eyelid on one side (the palpebral surface) and the cornea on the other side (the bulbar surface). Embedded in the bulbar surface is a dense array of lymphoid follicles—tiny compartments containing disease-fighting cells—that are in contact with the surface of the eye and with a thin layer of liquid called the tear film. The follicles function as the lymph nodes of the eye.

Between the two layers of the conjunctiva is a dense, T-shaped cartilage plate. The crossbar of this T cartilage stiffens the free edge of the third eyelid and curves to hug the corneal surface. Surrounding the stem of the T cartilage is a gland that produces much of the water component of the tear film. The gland releases these watery tears through tiny ducts between the lymphoid follicles on the inner surface of the third eyelid, replenishing the tear film while allowing the immune system to gain access to the ocular surface.

In cats, as in most mammals and birds, the third eyelid is large enough to completely cover the cornea and acts much like a windshield wiper—removing debris from the surface and redistributing tears over the cornea. When the cat is alert, the third eyelid is mostly hidden within the eye socket, with only a small portion visible in the inner corner of the eye. Yet when the cat is relaxed, during sleep or blinking, a set of skeletal muscles retracts the eyeball and allows the third eyelid to float across the ocular surface from the inner, lower corner of the eye to the upper, outer corner. Movement of the third eyelid in cats is also partially regulated by the sympathetic nervous system and by smooth muscle cells within the third eyelid.

THE REAL QUESTION IS NOT "WHY DO CATS HAVE A THIRD EYELID?" BUT "WHY DON'T PEOPLE HAVE A THIRD EYELID?"

The third eyelid's function is not fully understood, but it is believed to help protect the cornea from physical injury, especially when the cat is capturing prey or moving through dense vegetation. It also allows cats to produce more tears than primates do, perhaps to better moisten the much larger cornea of the feline eye. The lymphoid follicles covering the surface of the third eyelid dump antibodies and other immunological mediators into the tear film, bathing the ocular surface and protecting it from the stew of bacteria and fungi that inhabit the surface of any eye.

The third eyelid not only serves as a windshield wiper of sorts but also can be an easy-to-read gauge of the cat's overall well-being. When the membrane protrudes from its corner more than usual in both eyes, the expansion is often a sign of a generalized health problem or dehydration. Correct these problems, and the membrane returns to its normal position.

Experts also believe that the third eyelid helps to keep the surface of the eye moist, by holding the tear film against the cornea more tightly than the upper and lower eyelids alone. Loss of the third eyelid frequently results in chronic irritation of the cornea and the remaining conjunctiva.

So why don't humans have a third eyelid instead of a rudimentary fleshy bump in the inner corner of the eye? Although the exact reason is unknown, it may be related to the fact that humans do not typically capture prey by biting (as cats do) or find food by rooting through vegetation (as horses do). Thus, there may be no advantage for us in having this extra measure of protection for the eye's surface. *—Paul Miller*

Paul Miller is a clinical professor of comparative ophthalmology in the department of surgical sciences at the University of Wisconsin–Madison School of Veterinary Medicine.

JOHN DANIELS *age Fotostock*

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A Case for Cat Contraception

Strategies that prevent pregnancy without requiring surgery could improve the health of free-living cats

By Jessica P. Hekman

WHEN I WAS A VETERINARY STUDENT, I SOMETIMES found a big orange cat sunning himself on my front porch at the end of my workday. He always ambled away as soon as he saw me—not a panicked dash, because he was used to humans—but he certainly was not going to let me get close enough to pet him. No one owned this cat, although my next-door neighbors sometimes fed him, and he clearly lived in the neighborhood; he and my dogs knew one another well, interacting loudly across the fence.

He was a feral cat, otherwise known as a community cat. He probably lived in a small colony, and indeed I sometimes saw several other individuals around. This orange cat seemed to have a pretty good life, which is often true for cats living in colonies that get some food and other care from people. His life, however, was liable to be shorter than that of an owned cat; during my tenure in that neighborhood, I took two badly injured community cats to the local veterinary hospital for euthanasia. (As the area's veterinary student, I found that one of my de facto responsibilities was dealing with felines that had been hit by cars or attacked by other animals.)

He was also at risk of disease, such as feline leukemia or feline AIDS, because he had probably never been vaccinated. He was not the only one at risk: his colony may maintain a reservoir of these feline diseases that can then be transmitted into the population of owned cats that are allowed outdoors to interact with their feral cousins. Moreover, community cats are often sexually intact and certainly contribute to the overwhelming number of kittens that my neighborhood saw every spring and summer. And, of course, bird lovers complain of the depredations by feral cats on the local wildlife.

It used to be that people trapped community cats and brought them to animal shelters. The shelters had few options other than euthanizing the cats, which were unable to adapt to life as pets. This approach did not provide effective population control, however, because when a colony of cats was depleted, new cats would move in to take their place.

It turns out that maintaining a healthy colony keeps new cats out. In the past decade or so volunteers and animal shelters have been implementing trap-neuter-vaccinate-return (TNVR) programs. Teams trap cats and bring them to veterinary clinics, where they are vaccinated and spayed or neutered and then returned to their colonies, which are managed by caretakers. In this way, colonies are kept small but healthy. Although the remaining cats may still attack small animals, the alternative—trapping and euthanizing them—does not reduce the population of predators either.

Maintaining TNVR programs takes a lot of money, however. Veterinary surgeons are not cheap, and even when they volunteer to help, they still need access to a surgical suite. Cats have to be trapped on a specific day when a TNVR clinic is scheduled (not an easy task itself), transported to the clinic and then transported back. The expense slows the process. And in the end, it is not possible to spay and neuter cats fast enough to keep up with the population.

A simple medical intervention would be much more efficient than surgery. The ideal contraceptive would be inexpensive to make and easy to administer; a single treatment would have a long-term or even permanent effect; it would have a wide margin of safety for both cats and the environment (you would not want a dead cat to be full of some toxic substance that would endanger other animals); and it would act rapidly. The drug should pre-

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vent litters and reduce the nuisance behaviors associated with breeding because—let's face it—cats having sex are extremely noisy. Ideally many cats would receive and respond to the drug, although studies suggest that it needs to affect only 70 to 80 percent of female cats to achieve population reduction.

One promising approach is an immunocontraceptive, or birth-control vaccine, that works by evoking an immune response. Eliciting immune activity may sound like a strange way to prevent pregnancies, but vaccines do tend to work long term and are actually a logical choice for this situation.

The approach under study targets gonadotropin-releasing hormone (GnRH), the master switch of the reproductive system. Through minion hormones, GnRH controls production of testosterone, estrogen and sperm, as well as ovulation. Hence, eliciting an immune response against it should reduce both pregnancy and mating behaviors.

The idea is enticing: volunteers could trap cats, then dose them with the contraceptive and the usual array of antidisease vaccines right in the trap and release them, never having had to bring them to a veterinary clinic. A commercial GnRH-blocking vaccine, GonaCon, is approved in cervids and has been successfully used in white-tailed deer. It has been tested in cats only in laboratory settings so far, where the vaccine works somewhat unpredictably. Some vaccinated animals keep right on getting pregnant. How long it functions is also somewhat variable, but in one study a single injection prevented pregnancy in close to 90 percent of the animals for a year and remained effective for five years in almost a third of the cats.

Although your house cat might live into its late teens, several years of birth control are probably enough for shorter-lived community cats. Investigators at the University of Illinois at Urbana-Champaign and the University of Florida are now collaborating under the guidance of the Alliance for Contraception in Cats and Dogs (ACC&D) to evaluate GonaCon's effectiveness in the field.

Real life is never simple, of course. When I was a veterinary student, I discussed contraceptive vaccination with experienced veterinary assistants at an animal shelter. They loved the idea but pointed out that in Massachusetts, where I lived at the time, once you are providing any medical care for a cat, such as contraception, you have to make sure they are vaccinated for rabies.

Feral cats hang out in an alley.

ANDREI SPIRACHE *Getty Images*

Unfortunately, rabies vaccination legally requires the presence of a veterinarian, and once you have to bring in a vet, the expense starts going up again. We batted around some ideas—maybe you could distribute an oral form of a vaccine in bait form and get around the rabies vaccination requirement by dint of never actually touching the cat. But it seems that policy changes might be necessary in some states before immunocontraception could be widely used in community cats.

These contraceptives for feral cats are not quite ready for prime time yet, but studies are under way to move this important work forward. My suspicion is that the biggest problem is simply willingness on the part of society to commit the resources necessary to develop a workable solution. Cat rescuers and animal shelters, all of whom have notorious funding problems, cannot possibly represent attractive markets to drug companies. This situation leaves paying for the necessary research and advocacy for required policy changes up to private nonprofit organizations. You can stay up-to-date with news as the story unfolds at the ACC&D [see "More to Explore," below]. Community cats may be our responsibility, as domesticated animals gone feral, or they may not be, but either way they affect us and the animals with which we live. Efficient and humane management of their populations benefits both us and them. SA

Jessica P. Hekman is a veterinarian and a Ph.D. student at the University of Illinois at Urbana-Champaign, training in a genomics laboratory that studies a population of tame foxes. Her interests include the stress response in mammals, canine behavior, canine domestication, shelter medicine, animal welfare and open-access publishing. Hekman writes The Dog Zombie blog (www.dogzombie.com).

MORE TO EXPLORE

Contraceptive Vaccines for the Humane Control of Community Cat Populations. Julie K. Levy in *American Journal of Reproductive Immunology: Special Issue on Contraceptive Vaccines*, Vol. 66, No. 1; July 2011.

Long-Term Fertility Control in Female Cats with GonaCon™, a GnRH Immunocontraceptive. Julie K. Levy et al. in *Theriogenology*, Vol. 76, No. 8, pages 1517–1525; November 2011.

Contraception and Fertility Control in Dogs and Cats: A Report of the Alliance for Contraception in Cats & Dogs. ACC&D, February 2013. Available at www.acc-d.org/docs/default-source/Resource-Library-Docs/accd-e-book.pdf?sfvrsn=0

Alliance for Contraception in Cats and Dogs: www.acc-d.org

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Played by a Parasite

Toxoplasma gondii, an insidious and common parasite spread by cats, controls its rodent host's brain—and may be manipulating our own behavior as well

By Gustavo Arrizabalaga and Bill Sullivan

IMAGINE A WORLD WITHOUT FEAR. IT MIGHT BE EMPOWERING TO go about your daily life uninhibited by everyday distresses. You could cross highways with confidence, take on all kinds of daredevilry and watch horror flicks without flinching. Yet consider the prospect a little more deeply, and the possibilities become darker, even deadly. Our fears, after all, can protect us.

Illustration by Boris Séméniako

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The basic aversion that a mouse has for a cat, for instance, keeps the rodent out of death's jaws. But unfortunately for mice everywhere, there is a second enemy with which to contend, one that may prevent them from experiencing that fear in the first place. A unicellular organism (a protozoan), *Toxoplasma gondii,* can override a rodent's most basic survival instincts. The result is a rodent that does not race away from a cat but is instead strangely attracted to it.

Toxoplasma's reach extends far beyond the world of cat and mouse. It may have a special relationship with rodent and feline hosts, but this parasite also infects the brains of billions of animals on land, at sea and in the air. Humans are no exception. Worldwide, scientists estimate that as many as three billion people may be carrying *Toxoplasma*. In the U.S., there is a one-in-five chance that *Toxoplasma* parasites are lodged in your neural circuits, and infection rates are as high as 95 percent in other countries.

For most people, this infection appears asymptomatic, but recent evidence shows that *Toxoplasma* actively remodels the molecular landscape of mammalian brain cells. Now some researchers have begun to speculate that this tiny single-celled organism may be tweaking human health and personalities in stealthy, subtle ways.

WHAT THE CAT DRAGGED IN

RESEARCHERS FIRST DISCOVERED *T. gondii* in 1908, and by the end of the 20th century they had a good grasp on how people could pick up this parasite. The story starts with cats: for reasons that scientists have yet to unravel, *Toxoplasma* can sexually reproduce only in the feline gut. The parasite breeds within its feline host and is released from the feline's tail end. Cats are such obsessive groomers that it is rarely found in their fur. Instead people can become infected from kitty litter or by ingesting it in contaminated water or food [*see box on page 88*].

Within a new host the parasite begins dividing asexually and spreading throughout the host's body. During this initial stage of the infection, *Toxoplasma* can cause the disease toxoplasmosis in immunocompromised or otherwise susceptible hosts, leading to extensive tissue damage. Pregnant women are particularly at risk. If a woman is infected with *Toxoplasma* for the first time during pregnancy, the parasite may invade the developing fetus, cutting through tissues and organs as it spreads from cell to cell. Infection early in pregnancy can result in miscarriage or birth defects.

AFTER INFECTION, NEURAL ACTIVITY SHIFTS FROM THE DEFENSIVE TO THE REPRODUCTIVE PATHWAY. INSTEAD OF DANGER, THE RATS SMELL LOVE.

In otherwise healthy individuals, however, the only symptoms during this period are brief, flulike discomforts such as chills, fever and body ache. Within days the immune system gets the parasite under control, and *Toxoplasma* retreats into a dormant state. It conceals itself within a hardened wall in the host's cells, a structure called a tissue cyst.

This stage of the infection has no other discernible symptoms, but individuals with dormant infections who develop compromised immune systems—because of AIDS, an organ transplant or chemotherapy—may experience severe complications. With the body's defense systems weakened, *Toxoplasma* can reactivate and grow uncontrollably.

Once infected, a person will remain a carrier for life. Our immune system is apparently incapable of eliminating the tissue cysts, nor can any known drug. Nevertheless, the infection, detectable with a blood test, has long been viewed as relatively benign. After all, many people carry this parasite with no obvious ill effects. Only recently have scientists begun reexamining this belief.

EAT ME, MR. KITTY

IN THE 1980S RESEARCHERS noticed unusual behaviors in *Toxoplasma*-infected mice. The rodents became hyperactive and groomed less. In 1994 epidemiologist Joanne Webster, then at the University of Oxford, observed that rats harboring tissue cysts behaved differently from their uninfected counterparts. Instead of fleeing from cats, the infected rodents moved toward them—making them easier prey.

Webster suspected that this "fatal feline attraction," as she called it, was a crafty way for the parasite to get back into a cat's belly to complete the sexual stage of its life cycle. In the years to follow, this idea gained ground: a large body of work now shows that the parasite can indeed manipulate rodents' behavior by altering neural activity and gene expression.

Several well-controlled experiments have shown that although uninfected rodents avoid areas that have been infused with cat stench, infected rodents do not seem to mind. Even more bizarre, in 2011 neuroendocrinologist Robert Sapolsky of Stanford University, molecular biologist Ajai Vyas of Nanyang Technological University in Singapore and their colleagues found that—at least in terms of neural activity—infected rats appeared to be *sexually* attracted to cat scent.

In the mammalian brain, the "defensive" and "reproductive" neuronal pathways run in parallel. These pathways start at the olfactory bulb, involved in odor detection, and terminate at the limbic system, an area critical to basic reactions such as fear and arousal. Their proximity may partially explain how the parasite manipulates rodent behavior.

Working with 18 infected and 18 uninfected male rats, Sapolsky and his colleagues studied the rodents' behavior when they were exposed to either the

IN BRIEF

A feline parasite, *Toxoplasma gondii,* may inhabit the brains of as many as three billion people worldwide.
New molecular and cellular evidence suggests that the parasite has widespread and lasting effects on its rodent hosts.
Toxoplasma has the power to modify its host's brain and behavior, but to what extent this manipulation occurs in humans is still unclear. It may be changing human health and personalities in subtle ways.

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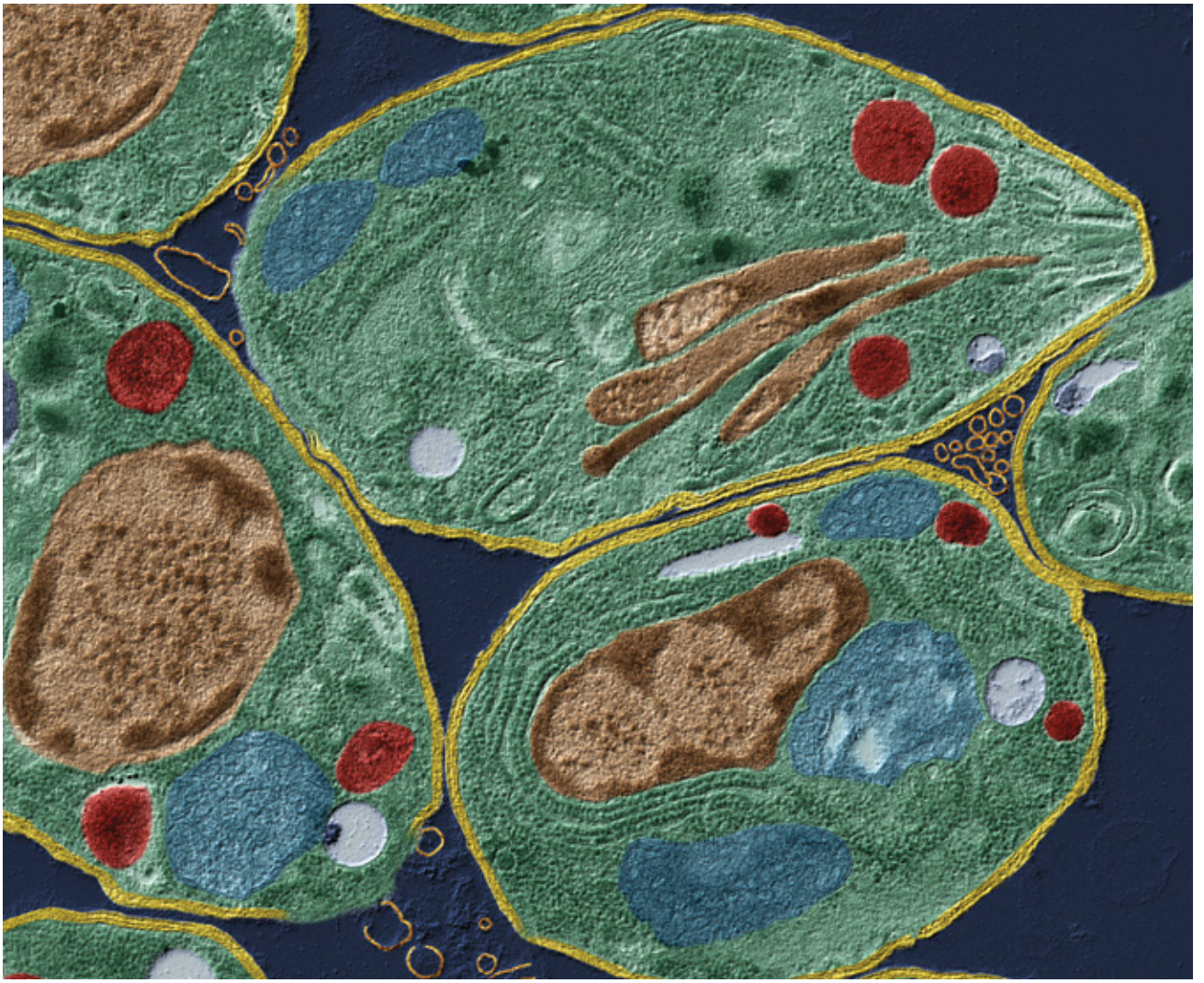

With powerful magnification, a colored transmission electron micrograph image reveals *Toxoplasma gondii* cells.

SCOTT CAMAZINE *Science Source*

odor of female rats or cat urine. Then they sacrificed the animals and looked at their brains. The researchers found a slight enrichment of parasite cysts in the limbic system compared with other brain areas.

They also assessed which parts of the brain had been operating during exposure to odors by staining the cells with a solution that revealed c-Fos, a protein expressed when neurons are active. The Stanford researchers discovered that infected rodents had high levels of engagement in their brain's reproductive pathway in response to the odor of both female rats and felines. In addition, the team found that infected rodents exposed to cat urine showed activation in the reproductive pathway similar to what uninfected rodents showed for the scent of a female rat. These results suggest that in infected rats, neural activity shifts from the defensive to the nearby reproductive pathway. Instead of smelling danger, the rats smell love.

Scientists are not sure how exactly the parasite elicits this fatal attraction, but one clue surfaced in 2014 in Vyas's laboratory. Vyas and his colleagues showed that *Toxoplasma* increases its host's levels of a neurotransmitter involved in social and sexual behavior. To accomplish this task, the parasite alters DNA methylation. Methylated genes are silent, blocked by a molecular cap. *Toxoplasma* uncaps a group of genes that spurs the creation of the sex-promoting neurotransmitter. Vyas and his team discovered this trick by performing the process in reverse: when they administered a chemical compound to the infected rats that silences the associated genes, the rats' peculiar attraction to feline odor vanished.

KISS AND SPIT

WITH EVIDENCE MOUNTING that *Toxoplasma* can influence its host's brain, other scientists set out to understand the parasite's effects at a much smaller scale: within each host cell. Their findings suggest that this microbe is particularly insidious—the changes it makes may be permanent.

To replicate, *Toxoplasma* must invade a cell. Stanford parasitologist John C. Boothroyd has dubbed this process "kiss and spit." The parasite first attaches to the host cell (the kiss) and then releases an arsenal of foreign proteins into that cell (the spit). *Toxoplasma* then enters the host cell, and the injected proteins help it redecorate its new home.

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The parasite's first act is establishing a protective bubble in which it can divide in peace without attacks from host cell proteins. (Later, during the infection's dormant stage, these bubbles thicken to become tissue cysts.) The parasite then moves the mitochondria, which serve as the cell's powerhouses, to be adjacent to the protective bubble. It also acts on the cell's DNA, inhibiting the expression of some host genes while activating others. Finally, *Toxoplasma* modifies host proteins to alter their function and inhibit the immune response.

Altogether, these modifications ensure that the host cell will live a long time and supply energy to the parasite, without alerting immune cells that a parasite has moved in. Although these findings have principally been made with rodents, work with human cell cultures suggests that the same changes probably take place in the human body. In our labs, we are studying how *Toxoplasma* replicates and interacts with its host in an effort to develop new drugs to treat this infection.

Remarkably, a study that Boothroyd's group published in 2012 showed that *Toxoplasma* not only spits into the cells it invades but also spits into cells that it does not infect. This behavior—spitting proteins in passing without lingering in the cells—is a recent discovery in the microbial world. Consequently, cells that are not harboring *Toxoplasma* contain parasite proteins that can co-opt and reprogram those cells. In the brains of infected mice, cells that have been spat into but not invaded are even more common than ones containing parasites. This widespread scattering of proteins means *Toxoplasma* can affect its host at a global level, making it easier to imagine how the parasite might manipulate the activity of an entire animal.

In 2013 biologist Michael Eisen of the University of California, Berkeley, and his colleagues found that a rodent's strange attraction to cat odors may be permanent, even if there are no longer signs of infection. In one study, Eisen exposed mice to a mutant strain of the parasite that does not appear to form brain cysts. Four months later the infected mice had no detectable parasites in the brain, yet they were still attracted to cat odors instead of repelled. This finding suggests that even if the parasite can be removed from the body, behavioral changes may persist. The infection leaves a mark, like a permanent parasite-given tattoo.

THE HUMAN CONNECTION

THE FACT THAT PEOPLE do not throw themselves into the lion cage at the zoo strongly argues that *Toxoplasma* does not affect humans in the way it transforms mice. Mammalian brains are not all the same, and *Toxoplasma*'s tricks are most likely specially suited for rodents. The parasite has little to gain, in evolutionary terms, by adapting to control the human brain. We are, after all, a "dead-end" host—the parasites within us are unlikely to return to the cat gut for breeding. Nevertheless, these cysts lodged in our brains could be manipulating us in subtle, unexpected ways. For example, a recent study by epidemiologist Angelico

LIFE CYCLES

How *Toxoplasma* Conquered the Animal Kingdom

Toxoplasma gondii is the most widespread parasite on earth, found across all continents and in a staggering variety of habitats. We have only recently discovered how many different animals it infects. To the surprise of many, University of British Columbia scientists found the parasite in beluga whales in the Arctic in 2014. Off the California coast, *Toxoplasma* infection has been revealed to be responsible for sea otter deaths formerly attributed to sharks or boats.

The wily intruder owes its success in part to a high rate of expansion. A cat newly infected with *Toxoplasma* can excrete up to 800 million packets containing the parasite—called oocysts—in the span of about seven to 14 days. Once released, an oocyst can persist in soil or water for years. Inhaling or ingesting just one oocyst is enough to establish infection, which virtually guarantees that the parasite will find its way into a variety of new hosts.

But house cats may have unfairly gotten a bad reputation from their link to *Toxoplasma.* Pet owners may indeed accidentally ingest an oocyst if they fail to wash up after tending to kitty litter, but scientists believe an individual cat will shed oocysts only once in a lifetime.

In contrast to housebound felines, wild and feral cats can spread oocysts in gardens, farms and water reservoirs, meaning they are likely to be greater contributors to *Toxoplasma*'s spread. Oocysts are commonly found in dirty water or on unwashed fruits and vegetables. The parasite does not infect plants, but its oocysts can remain on their surface unless they are carefully cleaned.

Moreover, many animals—including humans—are likely to become infected by eating raw or undercooked meat. Any animal infected by *Toxoplasma* will harbor tissue cysts for the rest of its life. When that tissue is eaten in, for instance, steak tartare, the parasite spreads into its new host. These clever methods of entering new hosts have allowed *Toxoplasma* to disseminate across the globe.

—G.A. and B.S.

LAUREN PUSCHAVER *Corbis*

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Mendy of the University of Iowa found a potential link between *Toxoplasma* infection in children and performance on cognitive exams. A large body of research, mostly conducted by parasitologist Jaroslav Flegr of Charles University in Prague, supports the idea that *Toxoplasma* harbors the potential to change human behavior. In a series of personality assessments spanning more than a decade and involving nearly 2,500 individuals, Flegr and his colleagues found that certain traits often coincide with a *Toxoplasma* infection. For example, infected men tend to be introverted, suspicious and rebellious, whereas infected women tend to be extraverted, trusting and obedient.

Using a simple reaction time test, Flegr has also found that infected individuals are slower to respond than uninfected peers. This lag may relate to another correlation he has identified. In a 2009 analysis of 3,890 military conscripts in the Czech Republic, those with latent toxoplasmosis who also had a negative blood type, meaning they lacked the protein RhD, were six times more likely to be in a fender bender than those who were *Toxoplasma*-free or who had a positive blood type. The function of RhD is unknown. Flegr's results suggest RhD somehow protects people against *Toxoplasma*'s effects, but how it does so remains a mystery.

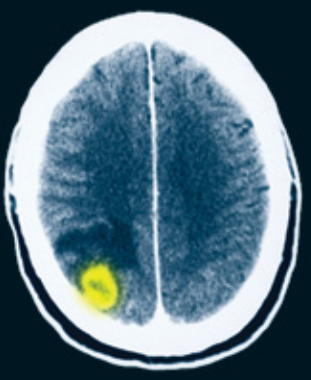
More recently, Flegr and his colleagues found that some of the changes that occur in mice also exist in humans—albeit in a gender-specific manner. In 2011 the researchers asked 34 *Toxoplasma*-infected students and 134 noninfected students to rate the intensity and pleasantness of urine samples from different animals. Curiously, infected men found cat urine odor more pleasant than uninfected men; in women, the opposite occurred.

Another line of research has focused on a potential link between toxoplasmosis and schizophrenia. In 2001 psychiatrist E. Fuller Torrey of the Stanley Medical Research Institute and neurovirologist Robert Yolken of the Johns Hopkins University School of Medicine reported significantly more antibodies associated with *Toxoplasma* in patients experiencing their first schizophrenic episode as compared with healthy peers. Although this initial study was limited to only 38 people, additional studies in the ensuing years have largely supported this link.

Fascinating and attention-grabbing as these studies may be, they come with several caveats. The sample sizes are relatively small, meaning the findings are preliminary. They do not definitively demonstrate that *Toxoplasma* causes behavior changes in humans. In the case of schizophrenia, it is important to note that the condition is complex and may involve many triggers. The parasite may be one contributor, but it is also possible that people with schizophrenia may simply behave in ways that make them more likely to pick up an infection. No hard evidence has emerged to date that directly implicates the parasite as a cause for any psychosis, including schizophrenia.

Ultimately these provocative findings probably reflect a complex exchange among various factors. Certain genetic predispositions, for example, or even an interaction between *Toxoplasma* and another infectious agent could mean that some people are more susceptible to the parasite's persuasion. Only larger studies from multiple research groups will determine precisely what this parasite may do to the people it infects. Expanded studies might also help explain why *Toxoplasma* appears to have the opposite effects in men and women.

BRAIN SCAN



Toxoplasmosis (*site of infection seen in yellow*) can cause serious complications in immunocompromised patients, such as this HIV-positive individual.

SCIENCE SOURCE

AN ACCIDENTAL MEDDLER

AS RESEARCHERS CONTINUE to uncover the astonishing effects that *Toxoplasma* has kept secret for so long, many scientists are beginning to think that *Toxoplasma*'s impressive cellular and molecular tricks make it capable of causing disruptions within a human host. At the very least, the findings from human surveys call for further clarification.

If you are curious whether you carry the parasite, you can get a blood test. In the meantime, you can increase your odds of staying *Toxoplasma*-free by maintaining good hygiene for you and your feline friends. If cats wander through your yard, the Centers for Disease Control and Prevention recommends wearing gloves and a mask when gardening and keeping any sandboxes closed up when not in use. Other basic health tips—cleaning fruits and vegetables, thoroughly cooking meats and washing hands regularly—are also important for avoiding an infection.

The notion that *Toxoplasma* could radically reorient the brain and behavior is certainly disturbing. But perhaps these findings are a reminder of a more basic truth. Each person actually constitutes a rich ecosystem. For every human cell in the body, there are 10 more bacterial cells that influence physiology, metabolism and health. The protozoan *Toxoplasma* is just another stowaway within the system and one that warrants more study. After all, we will never fully understand ourselves without learning about our microbial companions. SA

Gustavo Arrizabalaga and **Bill Sullivan** are professors of pharmacology and toxicology and of microbiology and immunology at the Indiana University School of Medicine. Each runs an independent research laboratory focused on the cellular and molecular biology of *Toxoplasma gondii*.

MORE TO EXPLORE

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THE SCIENCE OF DOGS AND CATS

The Emotional Animal

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Illustration by Bomboland

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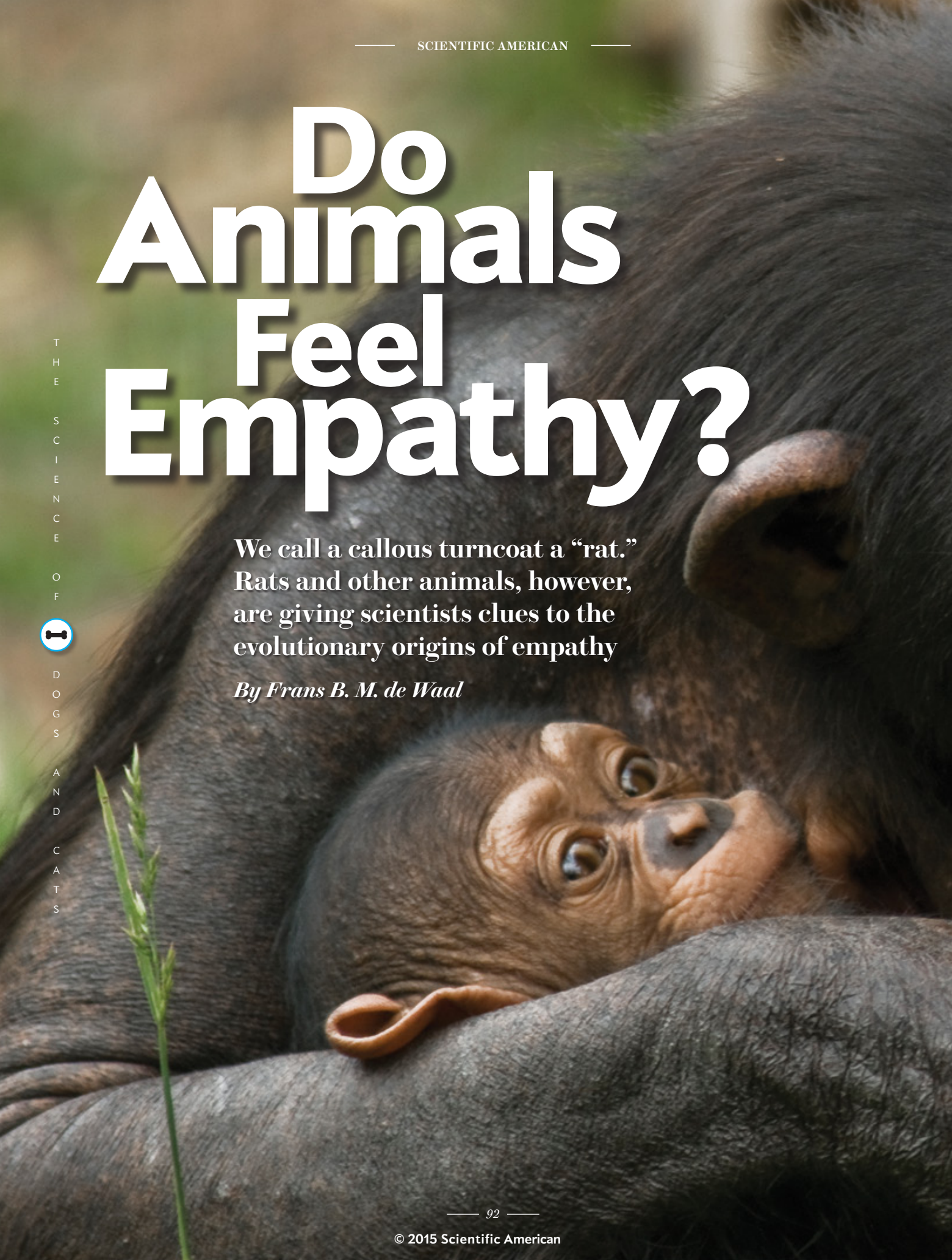
Do Animals Feel Empathy?

We call a callous turncoat a "rat." Rats and other animals, however, are giving scientists clues to the evolutionary origins of empathy

By Frans B. M. de Waal



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APART FROM SOME REAR-GUARD BEHAVIORISTS, FEW PEOPLE HESITATE TO ASCRIBE empathy to their dogs. But then dogs are man's best friend, freely credited with lots of human sentiments. For as much as we empathize with our canines, we have been stingy about recognizing empathy elsewhere in the animal kingdom, reserving it as a human trait. This belief is changing, however, as a growing line of research demonstrates not just empathy's existence in other animals but its subtleties and exceptions as well. And they shed some interesting light on how we developed our capacity for caring for others.

EARLY STUDIES

THE SURGE IN empathy studies during the past decade revives a line of research started about half a century ago. In 1959 a paper by psychologist Russell Church appeared in the *Journal of Comparative & Physiological Psychology,* provocatively entitled "Emotional Reactions of Rats to the Pain of Others." Church first trained rats to obtain food by pressing a lever. He found that if a rat pressing the lever saw another rat in a neighboring cage receive a shock from an electrified cage floor, the first rat would interrupt its activity—a remarkable result. Why shouldn't the rat continue to get food and simply ignore the other animal's flinching? The bigger question was whether the rats that had stopped pressing the lever were worried about their companions or just afraid that something bad might happen to them as well.

Church's work inspired a brief flurry of research during the 1960s that investigated the presence of "empathy," "sympathy" and "altruism" in animals. To avoid troublesome skepticism from colleagues, the investigators made sure to place the topics of their research in quotation marks; the prevailing behaviorist atmosphere made mention of animal emotions an anathema. Combined with the traditional emphasis on nature's nasty side, this taboo ensured that these studies went largely ignored.

In the meantime, however, human empathy became a respectable study topic. First, in the 1970s, came studies of empathy in young children; then, in the 1980s, in adults. Finally, in the 1990s, researchers began placing humans in brain scanners to monitor them while they watched others who were in pain or distress or who had a disgusted facial expression—revealing many intriguing findings about activity in the brain. This field now produces new articles every week. But for quite some time, animal studies lagged.

AN OLD SORROW

THIS SLUGGISH PACE began changing about nine years ago. Slowly but steadily, some 50 years after Church's rat study, the evo-

IN BRIEF

The study of empathy in animals, long discouraged by a behaviorist resistance to the attribution of human emotions to animals, is on the rise.

A landmark study found that mice that have witnessed other mice in discomfort or pain showed more sensitivity to pain themselves.

The mice typically showed more apparent empathy for cage mates that were familiar to them. Males (but not females) tended to show no signs of empathy for other males that were strangers to them.

This mouse study bolsters evidence that even rodents exhibit something akin to empathy—and strengthens the argument that empathy arises from basic neural mechanisms, yet to be fully understood, that human evolution has elaborated on.

PRECEDING PAGES: HELENA PAIXÃO *Getty Images*

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Two Camargue horses stand nuzzling.

If rodents show empathy, the capacity may be widespread indeed. A mouse study has indicated greater empathy toward cage mates than toward strangers.

SCOTT STULBERG *Corbis (horses)*; RENAUD VISAGE *Getty Images (mice)*

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lutionary origin of empathy became a hot topic, reviving interest in studies of whether animals experience this complex and socially vital connection to others. Psychologist Stephanie D. Preston of the University of Michigan and I have argued that a basic neural process, first developed in our animal ancestors, underlies even the sophisticated kinds of empathy that only we humans are capable of. Seeing another person in a certain situation reactivates neural representations of when we ourselves have been in similar situations; this brain activity, in turn, generates a body state resembling that of the object of our attention. Thus, to see another's pain may lead us to share it.

This empathetic capacity is in place on the very first day of a person's life. You can see it in any maternity ward, where all newborns will start crying as soon as one of them gets going. Artificial noise fails to cause the same reaction: babies are particularly sensitive to the distress calls of their own species. I have seen a similar spread of distress in young rhesus monkeys. Once, when an infant monkey had been bitten, it screamed so incessantly that it was soon surrounded by other infants. I counted eight of them climbing on top of the poor victim, pushing, pulling and shoving one another as well as the first infant. The response seemed automatic, as if the other infants were as distraught as the victim was and sought to comfort themselves as much as their companion.

The study of empathy in children started with measures of their reactions to a family member who had been instructed to cry. Very young children

WE EMPATHIZE WITH OUR PETS, BUT WE HAVE BEEN STINGY ABOUT RECOGNIZING EMPATHY ELSEWHERE AMONG ANIMALS.

Male lions greet each other.

NEURAL MECHANISMS

Empathy Is a Pain, So Why Bother?

By Peggy Mason

As Frans B. M. de Waal notes in the main article, the principles of biological continuity should make it unsurprising that mice act in empathetic ways similar to those seen in primates, including humans. The 2006 study by Dale J. Langford, then at McGill University, and her colleagues bolsters that view in striking ways.

For instance, it is tempting to explain empathetic behavior in animals that we believe to have only rudimentary cognition, such as mice, by arguing that the sight of a suffering fellow mouse simply evokes an automatic fear reaction. The Langford study undermines that explanation by finding that mice showed empathetic reactions only with cage mates; the mice seem to go far beyond being frightened by injury to accounting for whom the injured party is—friend, family, foe or stranger. This response is a significant step toward humanlike social feeling—caring for acquaintances more than for strangers, just as our empathy for someone who is hurt differs depending on whether the person is a foreigner, a national compatriot, a school chum or an immediate family member.

REFLECTION OF PAIN

So how can the brain accomplish empathy in general and empathy for pain in particular? One popular theory involves mirror neurons, discovered almost two decades ago by Giacomo Rizzolatti and his colleagues at the University of Parma in Italy. In Rizzolatti's original 1996 study, he and his colleagues found that premotor neurons in a monkey's prefrontal cortex—neurons that rou-

MARY McDONALD *Nature Picture Library*

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How can the brain accomplish empathy? One answer that is commonly put forward involves mirror neurons, brain cells (*such as the one depicted in the conceptual image at left*) that fire in response when a subject witnesses another animal or person perform a task—or experience pain.

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tinely fire as the monkey prepares a particular movement, such as reaching out to grasp something—fired in a similar pattern when the monkey merely watched the same task performed by another monkey or a human. The idea with respect to empathetically shared emotion is that affect-relevant neurons have mirror functionality, so that when an individual watches a loved one experience pain, these neurons discharge and create an affective state much like the viewer would feel if she were receiving the painful stimulus herself.

The notion that mirror neurons form the neural substrate for affective sharing is seductively attractive, but there are numerous fundamental problems with it. As articulated by Gregory Hickok in his book, *The Myth of Mirror Neurons* (W. W. Norton, 2014), any role for mirror neurons in empathy depends on these neurons being able to signal not only a motor action, such as reaching for a peanut, but also the intention behind that action—a desire to eat the peanut, for example. This is unlikely. The same movement may be used to achieve myriad different goals. At the time of an action, when the mirror neurons fire, the end goal of that action is yet to be revealed. Therefore, rather than coding for intention, mirror neurons may play a role in facilitating motor actions. A second major stumbling block for the hypothesis that mirror neurons are the basis for empathy is the lack of conclusive evidence for these neurons in any region of the human brain.

THE EMPATHETIC BRAIN

If mirror neurons are not responsible for sharing the pain experience between individuals, what is? For starters, it is clear that when it comes to pain, experiencing pain oneself and viewing another's experience of pain activate overlapping, but not identical, brain areas in humans. Work by psychology professor Jean Decety of the University of Chicago has showed that brain regions important in emotional arousal, such as the midbrain periaqueductal gray and the anterior cingulate cortex, are co-activated during self-pain more than during other-pain, although both regions are activated under both pain conditions. On the other hand, activation of the medial prefrontal cortex, a region critical to executive function and self-regulation, is more connected to activity in the anterior cingulate cortex during other-pain than during self-pain. Thus, despite the attractiveness of a paint-by-numbers interpretation of human brain-imaging data, individual brain areas do not determine individual emotional experiences. Instead circuits involving complex connections between specific areas of the brain shade our interpretation of our own feelings and others'.

The exciting work by Langford and her colleagues shows us that one mouse can discern the pain experience of another mouse and even alter its own behavior as a result. This may not be exactly the same as the other-oriented caring that one human offers to another human in pain, but it is one biological step closer to human experience than originally believed.

Peggy Mason is in the department of neurobiology at the University of Chicago. Inspired in part by writing this piece, she switched her scientific focus to empathetic helping in rats.

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would approach and touch or stroke the distressed relative. This reaction became known as empathetic concern.

Now we know that some animals will do the same. Researchers have observed consolation responses in dogs, elephants and primates. After one chimpanzee has attacked another, for example, a bystander will go over to gently embrace the victim until he or she stops yelping.

The tendency to console is so powerful that Nadezhda Ladygina-Kohts (also known as Nadia Kohts), a Russian scientist who raised a juvenile chimpanzee about a century ago, said that if her charge had escaped to the roof of her house there was only one way to get him down. Holding out food would not do the trick: the only way would be for her to sit down and sob, as if she were in pain. The young ape would then rush down from the roof to put an arm around her.

In bonobos, research has shown that empathetic concern is related to emotion regulation. The young bonobos that are best at coping with mental suffering (they scream less if frightened or distressed) are also the first to provide reassurance to others in distress. They are able to comfort others because of their better capacity to tamp down their own emotions. Emotional control is also a major factor in human empathy. There are so many similarities between humans and apes—including the tendency of females to exhibit empathy more readily than males—that the most parsimonious assumption is that the behavior in both species reflects the same mechanism, which may be as old as the mammals.

One of the most rigorous and particularly revealing studies of animal empathy came in 2006 from Dale J. Langford, then a psychology graduate student at McGill University, and her colleagues in a paper entitled "Social Modulation of Pain as Evidence for Empathy in Mice," published June 30, 2006, in *Science*. (Note that this time the word "empathy" is free of quotation marks; this absence reflects the growing consensus that emotional linkage between individuals probably has the same biological origin in humans and other animals.)

This study was inspired by a puzzle that Langford and her laboratory's director, pain geneticist Jeffrey S. Mogil, found intriguing: when they tested mice from the same home cage in experiments that involved light shocks to the feet, the researchers noticed that the order in which the mice were tested seemed to affect their pain response. The first mouse would always show fewer signs of pain than the last. Was the last mouse being sensitized to pain by seeing others in pain? Or was something else at work?

To find out, Langford, Mogil and their colleagues devised an experiment in which pairs of mice were put through a so-called writhing test. In each trial, two mice were placed in two transparent Plexiglas tubes so that they could see each other. Either one or both mice were injected with diluted acetic acid, which is known to cause a mild stomachache. Mice respond to this discomfort with characteristic stretching movements. (This is less a "writhe" than a sort of discomfited restlessness.) The researchers found that an injected mouse would show more of this movement if its partner displayed the same behavior than it would if its partner had not been injected. Most significantly, this increased display occurred only in mouse pairs who were cage mates.

Male (and not female) mice showed an additional interesting phenomenon when witnessing a strange male mouse in pain: its own pain sensitivity would actually drop. This counterempathetic reaction occurred only in male pairs that did not know each other, which are probably the pairs with the greatest degree of rivalry. Was the rivalry suppressing their reaction, or did they feel less empathy for a strange mouse?

(This gender effect reminds me of a wonderful study of human schadenfreude that Tania Singer, then at the University of Zurich, and her colleagues published in *Nature* in early 2006 (*Scientific American* is part of Springer Nature). The researchers found that in both men and women, seeing the pain of a person with whom one has just cooperated activates pain-related brain areas. But if a man felt he had been treated unfairly by another man in a previous exchange, his brain's pleasure centers would light up at seeing the other's pain. Such male antipathy toward rivals may be a mammalian universal.)

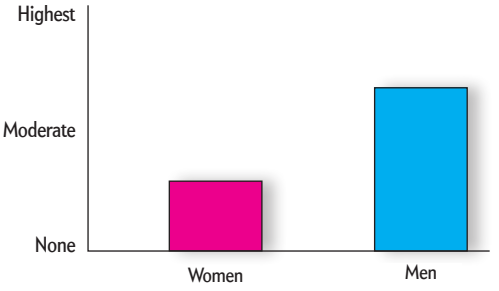
Finally, Langford and her colleagues also exposed pairs of mice to different sources of pain—the acetic acid as before

GENDER EFFECT

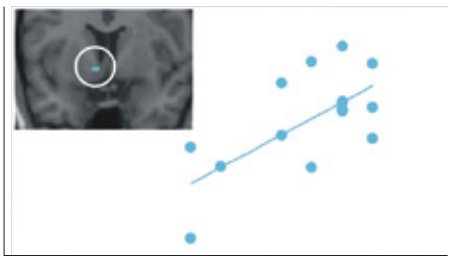
Turnabout Is Fair Play

Empathetic feelings can vary depending on context (*graphs*). In a study, men and women first cooperated with a partner and then saw that partner experience pain. In the men, pleasure centers in the nucleus accumbens (*blue spot in inset image at bottom*) activated if the partner had been unfair in the earlier exchange, indicating stronger feelings of revenge.

Self-Rated Feelings about Revenge



Pleasure Center Reaction



SOURCE: "EMPATHIC NEURAL RESPONSES ARE MODULATED BY THE PERCEIVED FAIRNESS OF OTHERS," BY TANIA SINGER ET AL., IN *NATURE*, VOL. 439; JANUARY 26, 2006. COURTESY OF TANIA SINGER (*inset*)

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and a radiant heat source that would cause pain if a mouse did not move away. Mice observing a cage mate suffering a stomachache withdrew more quickly from the heat source. In other words, the reactions of mice cannot be attributed to mere imitation, because a mouse seeing a companion in pain appears to be sensitized to *any* pain.

FOUNDATION OF EMPATHY

I ADMIRE THIS STUDY GREATLY. It is not the kind of manipulation we would nowadays apply to primates, but it goes a long way toward confirming the tentative conclusions of the 1960s, with the benefits of more subjects and more rigorous controls. Although it does not prove that the mice feel vicarious emotions, it demonstrates that they experience a vicarious intensification of their own experience.

This demonstration justifies speaking of "empathy" outside of humanity—at least in some instances. Here we find an interesting division between psychologists, who tend to think in terms of top-down processes, and biologists, who tend to think from the bottom up. The top-down view considers the most advanced forms of empathy, such as putting yourself into another's "shoes" and imagining his or her situation, and wonders how this ability arises; the inevitable answer is advanced cognition, perhaps even language. Yet merely imagining someone else's situation does not constitute empathy. Such imagination can be a cold affair, not unlike understanding how airplanes fly. Empathy requires emotional involvement.

Here the bottom-up view offers a better perspective. When we react to seeing someone display emotion and construct an advanced understanding of the other's situation, this process indeed involves—in humans and in some other large-brained animals—a great deal of cognition. But the emotional connection comes first; understanding and imagination follow. The mouse experiment suggests that the emotional component of this process is at least as old as our early mammalian ancestors and runs deep within us. SA

Frans B. M. de Waal is director of the Living Links Center at Emory University, where he studies the behavior and evolution of primates. He is author of *The Age of Empathy: Nature's Lessons for a Kinder Society* (Harmony Books, 2009).

DIALOGUE

The Author Answers Questions

As with most online news columns, Mind Matters at ScientificAmerican.com invites reader comments and questions. Unlike many such columns, however, inquiries often get answered by leading researchers—among them, the authors of posts about recent papers and other scientist visitors to the Web site—and by *Scientific American Mind* editors. The sampling below includes an exchange between readers and Frans B. M. de Waal. —*The Editors*

It's always baffled me that any anthropomorphism of animals is considered "unscientific" until the evidence supporting a particular instance is overwhelming. Occam's razor leads one to the opposite point of view. If we accept certain types of behavior as being motivated by particular emotional or mental states in humans, it follows that, barring good evidence to the contrary, the simplest assumption would be that similar behaviors are motivated by similar internal states in animals. Any argument that can be applied to dismiss this in animals applies equally to humans. Why the false dichotomy? It makes no sense. —*Kevin M.*

Put simply, Occam's razor relates to explanations and states that elements should not be multiplied beyond necessity. Animals being capable of empathy is by far more complex than if they weren't. There is absolutely no reason for us to assume any similarity between our behavior patterns and those of animals. To do so would be in violation of Occam's razor, not the other way around. To save ourselves confusion, it's best to wait for theories like this to be backed up by studies before contemplating what the theories might mean.
—*Nick Coad*

DE WAAL REPLIES:

*It's true that from a cognitive perspective, assuming empathy in animals is not particularly parsimonious. This is usually how Occam's razor is interpreted in psychology. That is a pre-Darwinian interpretation, however. I have argued elsewhere (*Philosophical Topics, *Vol. 27, pages 255–280; 1999) that there is a second kind of parsimony: evolutionary parsimony. This assumes that if two related species act similarly under similar circumstances, the simplest assumption is that the psychology behind their behavior is similar, too. The alternative would be to assume the separate evolution of similar behavior, which is not particularly elegant or economic. So, take your pick! I personally opt for the Darwinian version of Occam's razor.*

MORE TO EXPLORE

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When Animals Mourn

Mounting evidence from species as diverse as cats, dogs, giraffes and dolphins indicates that humans are not unique in grieving over the loss of loved ones

By Barbara J. King

ON A RESEARCH VESSEL IN THE WATERS OFF Greece's Amvrakikos Gulf, Joan Gonzalvo watched a female bottlenose dolphin in obvious distress. Over and over again, the dolphin pushed a newborn calf, almost certainly her own, away from the observers' boat and against the current with her snout and pectoral fins. It was as if she wanted to nudge her baby into motion—but to no avail. The baby was dead. Floating under direct sunlight on a hot day, its body quickly began to decay; occasionally the mother removed pieces of dead skin and loose tissue from the corpse.

When the female dolphin continued to behave in this way into a second day, Gonzalvo and his colleagues on the boat grew concerned: in addition to fussing with the calf, she was not eating normally, behavior that could be risky for her health, given dolphins' high metabolism. Three other dolphins from the Amvrakikos population of about 150 approached the pair, but none disrupted the mother's behavior or followed suit.

As he watched the event unfold in 2007, Gonzalvo, a marine biologist at the Tethys Research Institute in Milan, Italy, decided he would not collect the infant's body to perform a necropsy, as he would usually have done for research purposes. "What prompted me not to interfere was respect," he told me in 2013. "We were privileged to be able to witness such clear evidence of the mother-calf bond in bottlenose dolphins, a species that I have been studying for over a decade. I was more interested in observing that natural behavior than interrupting it by abruptly interfering and disturbing a mother who was already in obvious distress. I would define what I saw as mourning."

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Was the dolphin mother truly grieving for her dead calf? A decade ago I would have said no. As a biological anthropologist who studies animal cognition and emotion, I would have recognized the poignancy of the mother's behavior but resisted interpreting it as mourning. Like most animal behaviorists, I was trained to describe such reactions in neutral terms such as "altered behavior in response to another's death." After all, the mother might have become agitated only because the strange, inert status of her calf puzzled her. Tradition dictates that it is soft-hearted and unscientific to project human emotions such as grief onto other animals.

Now, though, especially after two years' research for my book *How Animals Grieve,* I think Gonzalvo was correct in his judgment that the mother dolphin was mourning. In recent years a critical mass of new observations of animal responses to death has bubbled to the surface, leading me to a startling conclusion: cetaceans, great apes, elephants, and a host of other species ranging from farm animals to domestic pets may, depending on circumstances and their own individual personalities, grieve when a relative or close friend dies. That such a broad range of species—including some quite distantly related to humans—lament the passing of loved ones hints that the roots of our own capacity for grief run very deep indeed.

DEFINING GRIEF

SINCE CHARLES DARWIN'S DAY, two centuries ago, scientists have debated hotly whether some animals display emotions beyond those associated with parental care or other aspects of survival and reproduction. Darwin thought that, given the evolutionary connection between humans and other animals, many emotions must be similar across species. He granted to monkeys, for instance, grief and jealousy, as well as pleasure and vexation. But the attribution of emotions such as these to animals fell increasingly out of mainstream scientific favor. By the early 20th century the behaviorist paradigm held sway, with its insistence that only observable behavior of animals, not their interior lives, could be studied with rigor. Gradually the scientific embrace of animal emotion has revived, thanks originally in part to anecdotes from long-term field studies on large-brained mammals. From Tanzania, Jane Goodall recounted in heart-wrenching detail young chimpanzee Flint's decline and death from grief only weeks after the death of his mother, Flo. From Kenya, Cynthia Moss reported that elephants attend to dying comrades and stroke the bones of deceased relatives. Field biologists and anthropologists began to ask questions about whether, and how, animals mourn.

To study and understand grief among animals, scientists need a definition that distinguishes it from other emotions. Whereas "animal response to death" embraces any behavior by an individual following the death of a companion animal, researchers may strongly suspect grief only when certain conditions are met. First, two (or more) animals choose to spend time together beyond survival-oriented behaviors such as foraging or mating. Second, when one animal dies, the survivor alters his or her normal behavioral routine—perhaps reducing the amount of time devoted to eating or sleeping, adopting a body posture or facial expression indicative of depression or agitation, or generally failing to thrive. For his part, Darwin conflated grief with sadness. But the two differ, primarily in intensity: the grieving animal is more acutely distressed, possibly for a more prolonged period.

This two-part definition is imperfect. For one thing, scientists lack a metric for evaluating exactly what counts as "more acutely distressed." Should the criteria for grief differ according to species, and might grief in other animals assume forms that are difficult for humans to recognize as mourning? The data are not yet available on these questions. Furthermore, mothers or other caretakers that constantly provide food or protection to infants that subsequently die cannot be said to have met the first criterion (going beyond survival-oriented behaviors), yet they remain among the strongest candidates for suffering survivor's grief.

Future studies of animal mourning will help refine this definition. For now, it furthers our critical assessment of responses made by animals when others around them die. For instance, baboon and chimpanzee mothers in wild African populations sometimes carry the corpse of their dead babies for days, weeks or even months—a behavior that on the surface of things might look like grief. But they may not exhibit any significant outward indicator of agitation or distress. When the animals carry on with their routine behaviors, such as mating, their behavior does not meet the criteria for mourning.

A MENAGERIE OF MOURNERS

A WIDE RANGE of species do exhibit behaviors that fit the two-part definition of grief, however, elephants among them. A particularly compelling example of elephant mourning comes from Iain Douglas-Hamilton of Save the Elephants and his team at Kenya's Samburu National Reserve, who in 2003 tracked elephants' responses to the dying matriarch called Eleanor. When Eleanor collapsed, a matriarch named Grace from another elephant family immediately came to her aid, using her tusks to support Eleanor back onto her feet. When Eleanor fell again, Grace stayed with her, pushing on her body, for at least an hour, even though her own family moved on. Then Eleanor died. During the course of the week that followed, females from five elephant families, including Eleanor's own, showed keen interest in the body. Some individuals appeared upset, pulling at and nudging the body with trunk and feet or rocking back and forth while standing over it. Based on the females' reactions (at no point during this period did a bull elephant visit the carcass), Douglas-Hamilton concluded that elephants show a so-called generalized response to dying and death—grieving not only for the loss of close kin but for individuals in other families.

Wild cetaceans also seem to exhibit a generalized grief response. In the Canary

IN BRIEF

Animal behaviorists have traditionally shied away from attributing human emotions, such as grief, to responses by animals.

But a growing body of evidence indicates that species ranging from dogs to dolphins mourn the passing of relatives and close companions.

These observations suggest that although the ways in which we mourn may be uniquely human, our capacity for grief has deep evolutionary roots.

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Dolphin mother carries the body of her dead calf on her dorsal fin in the waters off Dana Point, Calif.

COURTESY OF CAPTAIN DAVE'S DOLPHIN AND WHALE WATCHING SAFARI, DANA POINT, CALIF.

Islands in 2001 Fabian Ritter of Mammal Encounters Education Research observed a rough-toothed dolphin mother pushing and retrieving her dead calf's body in much the same way that the Amvrakikos dolphin mother later did with her baby's corpse. She was not alone: two adult escorts swam synchronously with her at certain periods, and at other times a group of at least 15 dolphins altered their pace of travel to include the mother and dead baby. The mother's persistence was remarkable, and when on the fifth day it began to wane, the escorts joined in and supported the infant on their own backs.

Giraffes, too, appear to grieve. In 2010 at the Soysambu Conservancy in Kenya, a female Rothschild's giraffe gave birth to a baby with a deformed foot. The baby walked less and remained more stationary than most calves. During the youngster's four weeks of life, wildlife biologist Zoe Muller of the Rothschild's Giraffe Project, based in Kenya, never saw the mother more than 20 meters away. Although individuals in a giraffe herd often synchronize their activities, foraging together, for example, the mother deviated from this pattern, preferring to stay close to the baby. Like the dolphin mother in the Amvrakikos Gulf, she may have risked her own health in doing so—though in this case for a living offspring.

One day Muller discovered the herd engaged in highly atypical behavior. Seventeen females, including the calf's mother, were vigilant and restless as they stared into a patch of bush. The calf had died in that spot about an hour before. All 17 females showed keen interest in the body that morning, approaching and then retreating from it. By the afternoon 23 females and four juveniles were involved, and some nudged the carcass with their muzzles. That evening 15 adult females clustered closely around the body—more closely than they had been during the day.

Throughout the following day numerous adult giraffes attended the infant's body. Some adult males approached for the first time, although they showed no interest in the carcass, instead focusing on foraging or inspecting the reproductive status of the females. On day three Muller spotted the mother giraffe alone under a tree about 50 meters from where the calf had died. The body itself, however, was no longer in its resting spot. Following a search, Muller located it, half-devoured, in the spot under the tree where the mother had been earlier. By the next day the body was gone, taken by hyenas.

Giraffes are highly social animals. After caching a newborn out of sight for about the first four weeks of life, the mothers sometimes engage in a crèche system in which one looks after the infants while the others forage. Muller does not use the words "grief" or "mourning" in describing the incident she witnessed. Yet this case is especially instructive. Not only the mother's behavior but also that of many of the females in her herd changed significantly in the wake of the infant's death. Although it is impossible to rule out an alternative explanation, the fact that the females had mounted a protective response against predators taking the baby makes it overwhelmingly likely that grief was involved.

Detailed observations of wild populations of animals, such as the ones Muller reported, are still relatively rare, for several reasons. Scientists may not be at the right place at the right time to observe postdeath responses by survivors. And even when they are present, no remarkable grief behaviors may ensue. Especially at this early stage of research into animal grief, observations from sanctuaries, zoos and even our own homes may supply needed clues.

I cannot imagine describing the behavior of Willa the Siamese cat without invoking the word "grief." For 14 years Willa lived with her sister, Carson, at the home of Karen and Ron Flowe in Virginia. The feline siblings groomed each other, lazed together in favorite parts of the house and slept with their bodies en-

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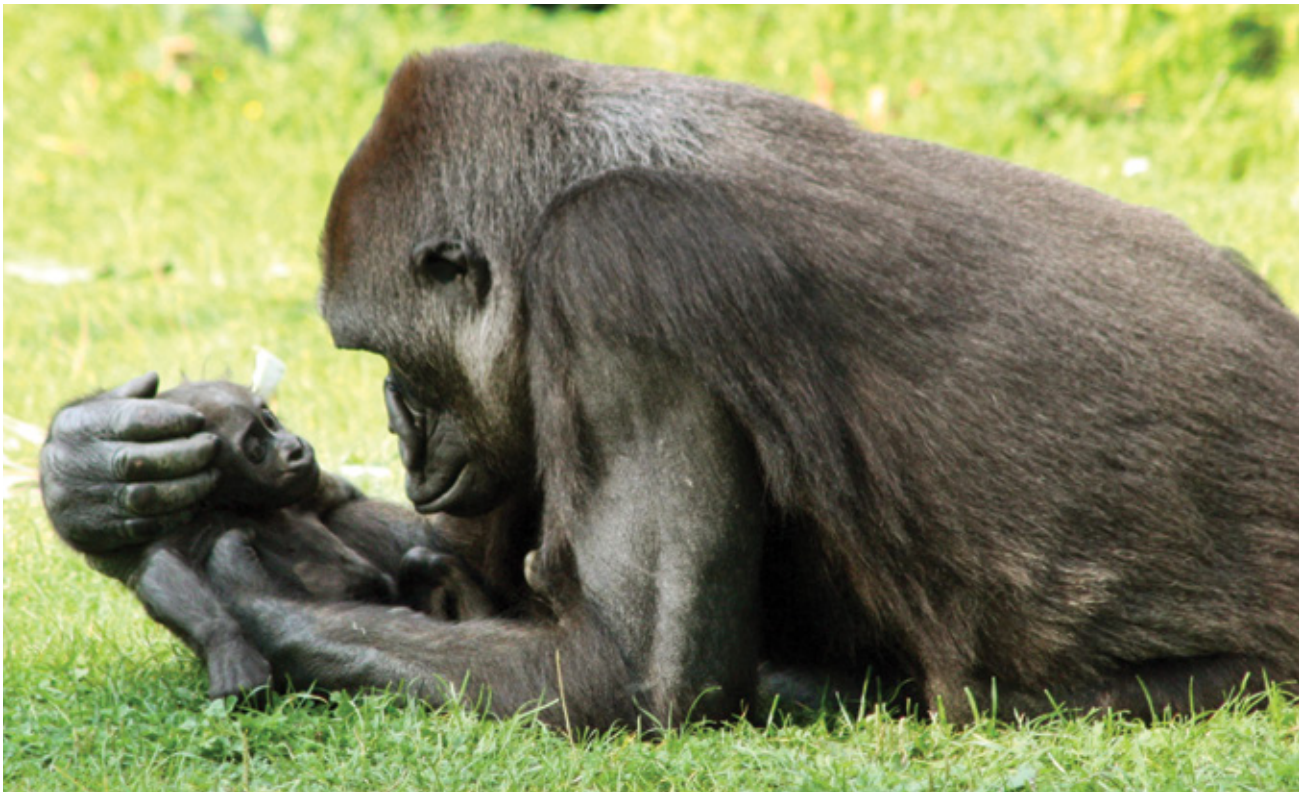

Female gorilla clutches her dead baby in a zoo in Münster, Germany. Although such behavior is not sufficient to demonstrate mourning, mothers who lose infants are among the strongest candidates for experiencing survivor's grief.

ALAMY

twined. If Carson was taken from the house to visit the vet, Willa acted mildly agitated until she reunited with her sister. In 2011 Carson's chronic medical issues worsened, and the Flowes took her again to the vet, where she died in her sleep. At first, Willa acted as she did when her sister was away for a brief period. Within two or three days, though, she began to utter an unearthly sound, a sort of wail, and to search the spots she and Carson had favored together. Even when this startling behavior faded, Willa remained lethargic for months.

The loyalty of dogs to their human companions is legendary, and so may be their grief. Visitors to Tokyo sometimes make a pilgrimage to the Shibuya train station to view a statue of an Akita named Hachikō, who waited daily for more than a decade for his human friend Hidesaburō Ueno to step off a train. Ueno, a professor who had died suddenly at his university office, would never again walk home with Hachi (as the dog was nicknamed), but the dog maintained a hopeful vigil until his own death. This profound loyalty is also found in dog-dog friendships. The ASPCA's Companion Animal Mourning Project reports that two thirds of dogs show behavioral changes indicative of emotional upset, lasting up to six months, when another dog in the same household dies.

These statistics reflect my family's experience. My cousin Connie Hoskinson's silky terrier, a tiny dog called Sydney, grieved twice over: for Connie's husband, George, when he died and later when her second dog, Angel, adopted when Sydney was 13 years old, suffered a sudden fatal heart attack. Without his canine friend—with whom he had slept and for whom he searched the house for weeks—Sydney ate less, lost weight and before long died in his sleep.

THE SORROW CONTINUUM

IT IS LOGICAL to think that long-lived species whose members partner most closely with others in tight-knit pairs, family groups or communities may more readily mourn the deaths of loved ones than other species do. But researchers do not yet know enough about animal grief to make such a claim. We need to test this hypothesis by systematically comparing responses to death in a variety of animal social systems, from gregarious ones to those in which animals come together only seasonally for food or mating.

Still, species-level differences in grieving will not be the whole story, because variation in the immediate social contexts and personalities of individual survivors will complicate matters. For instance, whereas the practice of allowing a survivor to view the body sometimes seems to prevent or reduce a period of distressed searching and vocalizing by the surviving animal, other times it seems not to help at all—attesting to the degree of individual variation in death responses within species. Likewise, evidence for grief in wild monkeys that live in cohesive social units is surprisingly limited so far, whereas in more solitary species such as domestic cats, bonds may develop between two or more kin or friends such that grief responses rival those of much more social animals. I predict that field observations will show that some monkeys across varied social systems visibly mourn as much as some domestic cats. Indeed, in *How*

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Animals Grieve, I recount examples from rabbits, horses and birds, as well as the other animals discussed here. In each species I find a grief continuum, with some individuals seeming indifferent to a companion's death and other individuals appearing distraught over such a loss.

Cognitive differences also play a role in animal grief. Just as there are different levels of empathy expressed by different species and even across individuals within a species, there must be varying levels of comprehension when animals grieve. Do some animals grasp death's finality or even have a mental concept of death? We simply don't know. No evidence suggests that any nonhuman animal anticipates death in the way we humans do, a capacity that underlies so much of our compelling literature, music, art and theater—and that causes our species a great deal of emotional suffering.

Indeed, the capacity to mourn may become quite costly for any animal in both physical and emotional terms, especially in the wild where alert high-energy behavior is needed for foraging, predator avoidance and mating. Why then did grief evolve in the first place? Perhaps the social withdrawal that often accompanies an animal's grief, if not taken too far, allows time for rest and thus an emotional recovery that in turn leads to greater success in forging a new close bond. Or, as John Archer writes in *The Nature of Grief,* it may be that "the costs involved in grief can be viewed as a trade-off with the overall benefits conferred by separation responses" seen when two individuals are keenly attached but forced apart from each other.

Under such circumstances, the missing partners may search for each other and thereby reunite and live to see another day. What is adaptive, then, may not be grief itself but instead the strong positive emotions experienced before grief comes into the picture, shared between two or more living animals whose level of cooperation in nurturing or resource-acquisition tasks is enhanced by these feelings.

THE PRICE OF LOVE

FROM THIS PERSPECTIVE, we may link grief with love, full stop. That is to say, grief results from love lost. Exploring emotions in a variety of species, ecologist and animal behaviorist Marc Bekoff of the University of Colorado Boulder embraces the idea that many animals feel "love" as well as "grief," even as he acknowledges that those concepts are hard to define precisely. We humans, he notes, do not fully understand love, but we do not deny its existence—or its power to shape our emotional responses.

In his book *Animals Matter,* Bekoff tells the story of a coyote called Mom whom he observed for several years during behavioral studies in Wyoming's Grand Teton National Park. At one point Mom began to make short journeys on her own away from her pack. Her offspring would rejoice when she returned: they licked Mom and rolled over exuberantly at her feet. Then Mom left for good. Some of the coyotes in her pack paced; others searched for her, setting off in the direction Mom had departed. "For more than a week some spark seemed to be gone," Bekoff writes. "Her family missed her." Discussing this with me, Bekoff attributed the family's response to its love for Mom. Generally, the potential for love is strong in species such as coyotes, wolves and many birds, including geese, he said, because male and female partners defend territories, raise their young together, and miss each other when they are apart.

LOVE IN THE ANIMAL WORLD OFTEN ENTWINES WITH GRIEF IN AN ACUTE MUTUALITY.

Love in the animal world often entwines with grief in an acute mutuality. Perhaps even more than the degree of social cohesion within a species, it is love between individuals that predicts when grief will be expressed. Can there be any real doubt that Willa, a representative of a species (the domestic cat) not known for its social nature, loved her sister, Carson, or that as the sole surviving sister, she suffered grief in the wake of her loss?

In our own species, grief increasingly became expressed through rituals rich in symbolism. By around 100,000 years ago, our *Homo sapiens* ancestors decorated dead bodies in red ocher, a behavior interpreted by archaeologists to be a kind of symbolic (rather than functional) ornamentation. At a site in Russia called Sunghir, two children younger than 13 years, a boy and a girl, were buried 24,000 years ago, together with elaborate grave goods ranging from mammoth tusks to animals carved from ivory. Most astonishing were the thousands of ivory beads found in the pair's grave, probably sewn onto the clothing (long since disintegrated) in which the children were buried. A good portion of this ancient human community at Sunghir must have come together in preparing this funeral ritual—each bead alone took an hour or more to manufacture. Although it is risky to project modern emotions onto past populations, the examples of animal grief reviewed here strengthen an emotion-based interpretation of the archaeological evidence: our ancestors of many thousands of years ago mourned their lost children.

In our modern world, grief is no longer inevitably confined to kin, close social partners or immediate members of one's own community. Public commemoratives at the Peace Memorial Park in Hiroshima; the genocide memorial center in Kigali, Rwanda; the Foundation Memorial to the Murdered Jews of Europe in Berlin; the site of the Twin Towers in Manhattan; or the Sandy Hook Elementary School in Newtown, Conn., all convey visibly the power of agonized global mourning. Our human capacity for sorrow at the deaths of strangers is built on an evolutionary substrate. Our own ways of mourning may be unique, but the human capacity to grieve deeply is something we share with other animals. SA

Barbara J. King is a professor of anthropology at the College of William and Mary. Her studies of monkeys and apes have led her to examine emotion and intelligence in a wide range of animal species.

MORE TO EXPLORE

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The Social Genius of Animals

New research reveals that animals interact in surprisingly sophisticated ways

By Katherine Harmon Courage

IN BRIEF

Only recently have researchers realized the extent of animals' social intelligence—their ability to understand and learn from others.

Animals may teach one another important skills, such as how to use tools.

Some critters can deceive. Intuiting what others know enables an animal to trick another member of the same species for personal gain.

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AT THE THAI ELEPHANT CONSERVATION CENTER, TUCKED AWAY IN THE TREES NEAR Chiang Mai, a pair of Asian elephants gazes at two bowls of corn on the other side of a net. The corn is attached to a sliding platform, through which researchers have threaded a rope. The rope's ends lie on the elephants' side of the net. If only one elephant pulls an end, the rope slides out of the contraption. To bring the food within trunk's reach, the elephants have to do something only humans and other primates were until recently thought to do: they must cooperate. Working in synchrony, each elephant grabs its end of the rope in its trunk and pulls, drawing the platform and the treats within reach.

Six pairs of these large animals succeeded in solving this double rope puzzle. A lone elephant would wait as long as 45 seconds for a partner to arrive, showing it knew it needed a buddy to get the job done. Psychologist Joshua M. Plotnik, now at Mahidol University in Thailand, and his colleagues, who documented these findings in 2011, also noticed that the elephant duos used different strategies for obtaining the food, suggesting that the animals had developed a deep understanding of social cooperation.

In the past century animals have repeatedly surpassed our expectations for their intellect. Koko the gorilla learned sign language; Alex the African grey parrot boasted a spoken vocabulary of more than 150 words; and even invertebrates such as the octopus have been seen using tools in the wild. Until the mid-20th century, we assumed only humans could use tools and learn meaningful pieces of a language. Sophisticated social skills such as cooperation were presumed to be way beyond animals' cognitive reach. Only recently have researchers begun to realize the extent of animals' social intelligence, their ability to understand and learn from others.

The latest findings suggest that some animals are not only capable of creating social connections but that many use them for survival. As with people, some animals have social needs. They notice when another member of their species is distracted, and they are able to figure out an effective way to get its attention. Animals may teach one another important skills, such as how to use tools. Some critters can even deceive. Intuiting what others know enables them to trick one of their kind for personal gain. The animals described below have some of the most impressive social abilities in the animal kingdom. Studying how they interact is giving scientists new insight into what they know—and a glimpse at what might be the upper limits of animal intelligence.

MAKING CONNECTIONS

IN OUR OWN LIVES, social intelligence might seem to play second fiddle to, say, the ability to do calculus or write a book. Individuals held up as modern geniuses, however, such as Stephen Hawking or the late Steve Jobs, have not only exceptional analytic skills but also an extraordinary ability to relate their ideas to a broader audience. These social skills are fundamental to our complex society. Without the ability to form a cohesive group, communicate ideas or collectively solve problems, humans could not have built the great pyramids or the first supercomputers.

DOGS SEEM TO NOTICE WHETHER A DOG THEY WANT TO PLAY WITH IS READY TO RECEIVE THEIR PLAY SIGNAL. THEY SEEM TO REACT TO DISTINCT COGNITIVE STATES OF OTHER DOGS.

Social skills require, first, a basic affinity for others. "You can't evolve all of the computational systems for social intelligence until you have that tendency that you want to be close to others," says biologist Louis Lefebvre of McGill University. Not all animals have this. Octopuses, for example, seek one another out only to procreate.

In contrast, zebra finches form monogamous pairs and congregate in groups. In a 2009 study the late biologist James Goodson of Indiana University Bloomington and his colleagues drilled down to the chemical essence of this social instinct: mesotocin, the bird equivalent of the human hormone oxytocin, which is implicated in bonding. When the researchers blocked mesotocin in the brains of the birds, they shrugged off their fellow finches. Females spent less than one third as much time near their same-sex cage mates after the treatment than before it. Extra doses of mesotocin had the opposite effect: the birds became even more social than they typically are.

Goodson and his colleagues also examined the biology of this hormone in other species of finches with different degrees of social affinity. The team found fewer receptors for mesotocin in key spots of the brain in species that were more territorial (less social) than the ze-

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bra finch—and more receptors in species that traveled in flocks. Scientists have identified similar patterns of brain chemicals and social preferences in many mammals. In prairie voles, for example, how mates bond with one another and their children is also associated with different levels of oxytocin and vasopressin, another hormone linked to social behavior and bonding.

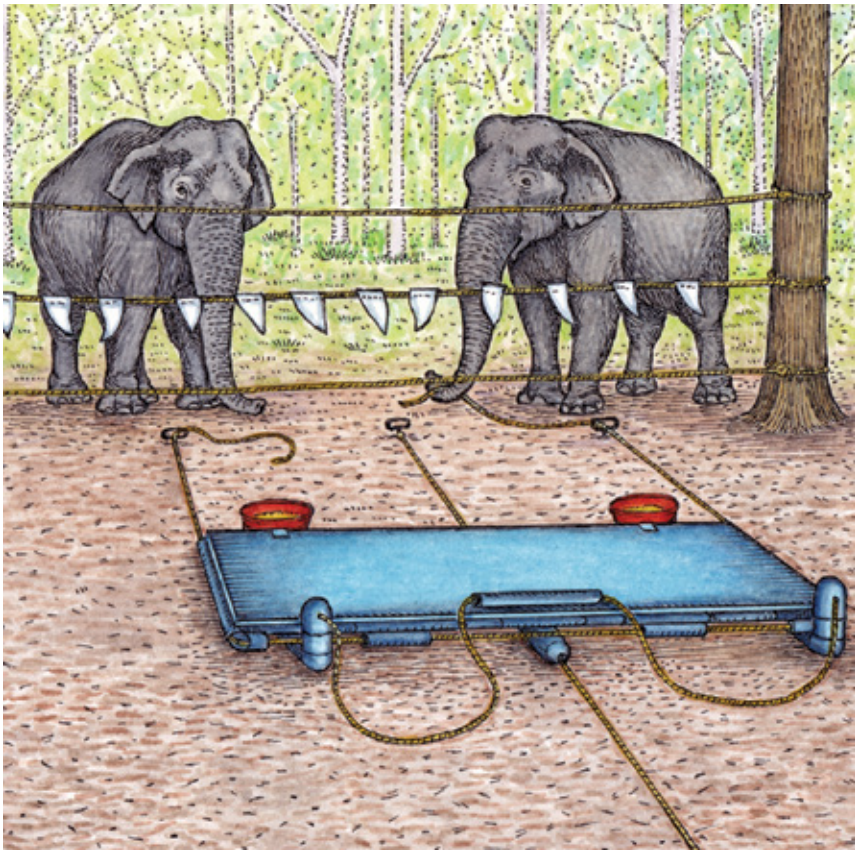
KNOW YOURSELF—AND OTHERS

GOOD SOCIAL GRACES also require a sense of the self as distinct from others. This primitive level of self-awareness allows animals to go beyond acting out a programmed set of behaviors for mating or for defense.

Researchers test self-awareness by placing a visible mark on an animal and showing it a mirror. An animal passes the test if it appears to recognize that the dot is on its body as opposed to on the "other" animal in the mirror. It can signal this awareness, for example, by reaching toward the spot on its own body. Great apes, elephants, bottlenose dolphins, orcas and magpies have all passed, suggesting they have more social prowess than animals that simply flock or school together.

The second requirement for social networking is an understanding that others have different mental states—knowledge, desires, beliefs or intents—and that at any given moment another individual might be in a mental state that is different from the one you are in. This ability is called theory of mind. Psychologists often test its development in young children by having a child and an adult observe a researcher place an object in a specific location, say, a ball in a cup. The adult leaves the room, and the ball is moved. After the adult returns, a child with a mature theory of mind understands that the adult does not know the ball has moved, and he or she does not expect the adult to look for it in the new location. Similar theory-of-mind tests are difficult to conduct in animals because it is hard to communicate with them directly.

Nevertheless, we can glean hints from their physiology, such as the presence of so-called mirror neurons. These cells, which have been found in macaques and birds, swing into action when an animal sees another individual doing something. In humans, they are thought to exist in various brain regions, including the supplementary motor area, a small patch of tissue at the top of the head that helps to control movement. Because these cells' activity patterns mirror the behavior of others and to some extent reflect the movement's goal, they may enable animals to understand others' actions, possibly even their intentions. They might underlie the ability to learn motor actions by observation and also buttress a theory of mind.



An elephant pair can slide bowls of corn within reach if they work together, each pulling one end of a rope. Dogs have been shown to cooperate similarly.

Mirror neurons have not yet been discovered in dogs, but more than a decade ago psychologist Alexandra Horowitz of Barnard College collected behavioral data suggesting that dogs may have some version of a theory of mind. Over the course of 21 months Horowitz videotaped a random sampling of dogs at play in a San Diego dog park. When she analyzed the footage, she noticed some interesting behaviors that suggested dogs could be aware of another dog's perspective.

The dogs at the park varied how they signaled a desire to play depending on the other dog's position. If a prospective playmate was already facing it, the dog gave a visual signal—opening its mouth wide or bowing down into that familiar bottom-up play pose. But if the other dog was turned away and otherwise engaged, it might instead give its friend a little nip. "They seem to be noticing whether a dog they wanted to play with was ready to receive their play signal," Horowitz says. "They seem to be reacting to distinct cognitive states" of others. In a paper published in 2011 Horowitz posited that dogs possess at least a rudimentary theory of mind.

Consistent with the mirror neuron findings, many monkeys and some birds have demonstrated in their behavior at least some capacity for theory of mind. Monkeys, birds and dogs are exceptions, however. In most animal species, scientists have failed to see even a glimmer of evidence for this advanced social capacity.

SCHOOLS AND STUDENTS

AMONG ITS MANY BENEFITS, social intelligence confers the ability to distribute information. Scientists have long observed

Illustrations by Patricia J. Wynne

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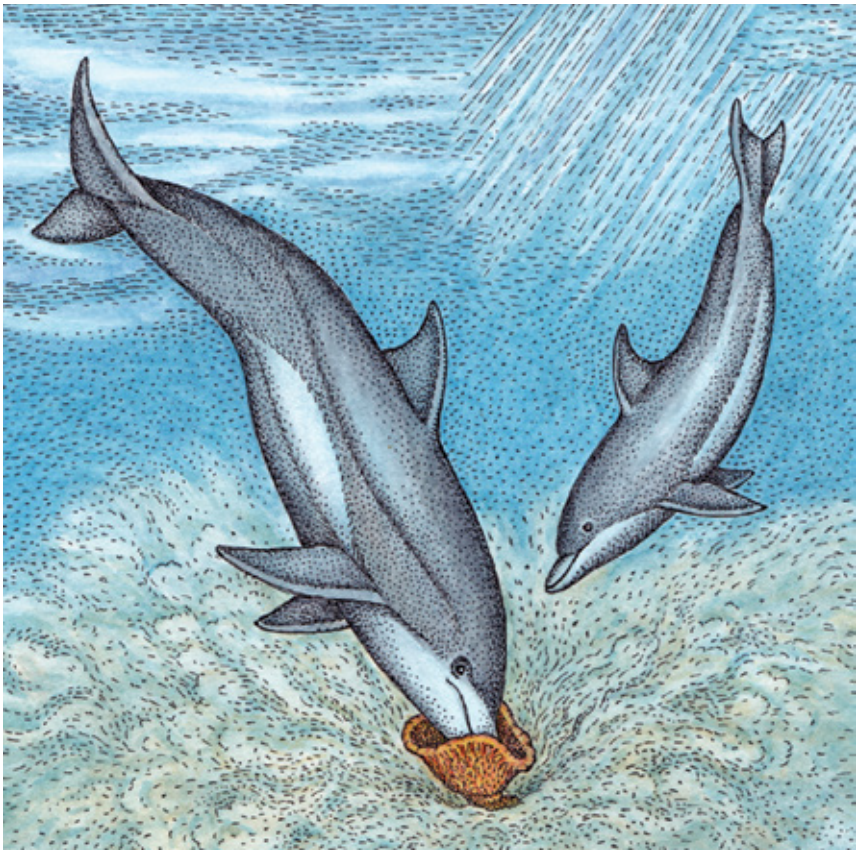
that herd animals can give warning signals if a predator is approaching; for example, a white-tailed deer may flash its conspicuous white tail, pointing it upward before bolting. Now, however, researchers are noticing that some animals that live in groups can teach one another rules of social engagement or ways to create a tool.

Zebra fish, for example, seem to transmit subtle social cues to other members of their school. These small creatures can make an easy meal for larger fish in the wild, so they tend to be cautious of new objects. If they are reared in captivity, however, they show little fear of a moving object, swimming within close proximity of it.

A team of researchers led by biologist Sarah Zala of the Konrad Lorenz Institute of Ethology at the University of Veterinary Medicine in Vienna wanted to know if these fish would change their behavior if surrounded by others that acted differently. The group introduced some shy, wild zebra fish to more brazen domestic ones. The wild ones learned from their new acquaintances to be bolder when a moving object was introduced near the tank. Instead of swimming away from it, they joined their fearless new companions and ventured toward it. When the emboldened wild fish were separated from their new friends, they still bravely swam near novel things. The results, published in June 2012, indicate these fish had not just mindlessly followed the other fish but had learned a new behavior.

Dolphins can convey more intricate behaviors to others. One group of bottlenose dolphins in Australia uses a technique called sponging to find food. Biologist Janet Mann of Georgetown University and her colleagues saw the females sporting a sea sponge on their snout, a technique that seemed to allow the dolphins to push along the seafloor to look for fish and other food without hurting their nose. The scientists sampled DNA from these sponging mammals and compared it with DNA from area dolphins that did not use this tactic. They discovered that the sponging dolphins, but not the others, had a common maternal line. In a 2008 report of the findings, the researchers suggested that mothers in this particular group managed to teach this complex act to their daughters.

Mother chimpanzees also use social learning to hand down wisdom to daughters. Young female chimps at the Gombe National Park in Tanzania are much handier at making tools to retrieve termites than are males. Adult females there use long twigs or stems to fish out termites, whereas males are more likely to kill larger game for their meals. In a study published in 2004, Elizabeth Lonsdorf of the Lincoln Park Zoo in Chicago and her colleagues found that the younger females spent more time with their mothers learning this skill than did the males, who were more likely to be playing—perfecting their social skills for later battles for dominance, mates and food.



One study suggests that certain dolphin mothers teach their daughters to don a sea sponge on their snout to guard against injuries while they scour the seafloor for food.

DECEPTION

SOCIAL LEARNING can be a big advantage for a group or species, which can transmit the most successful strategies to others. Some animals, however, use their social awareness for personal gain by hiding information from potential competitors. A group led by psychologist Federica Amici, then at Liverpool John Moores University in England, trained low-ranking capuchin monkeys, long-tailed macaques and spider monkeys to unlock a box to obtain a food reward. When alone, these monkeys unlocked the box and indulged. But when a dominant monkey was around, the trained animals—especially the macaques—chose to forgo the hidden treat, ignoring the box so as not to reveal how to open it.

Some species of birds engage in a similar type of deceit, bolstering the argument that these animals might also possess some theory of mind. Whether in a laboratory or the wild, Western scrub jays are more likely to move their food stashes when other birds are around. In fact, lab experiments have shown that scrub jays will either move or pretend to move a newly caught worm if they think another bird might have seen them bury it. This behavior suggests some awareness of what the other individual knows and how they can protect their own interests. "Nonprimate species are thinking about these things in some very clev-

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When a scrub jay spots another bird eyeing its food stash, it will move or pretend to move its edibles, indicating that these birds are cognizant of what their fellow jays know.

er ways," says psychologist Laurie Santos of Yale University.

At least one of the cooperating Asian elephants in Plotnik's experiments also learned how to game the social system. The elephant, named Neua Un, figured out that instead of pulling on her side of the rope, she could stand on her end so it would not slip. Then she let the other elephant do all of the hard work. She also moved her trunk every now and then, as if to convince her partner that she, too, was pulling.

EMOTIONAL APTITUDE

OF COURSE, SOCIAL IQ involves more than knowing how to get another person's attention or teaching the young new information and skills. A deeper social intelligence, one that allows for empathy and grief, is arguably the intangible, almost indescribable fiber that weaves us together. It is tied to our emotional well-being, and as new studies about longevity are showing, these rich social connections are important to our physical health as well. Although we might not be able to ask animals directly how they think and feel about others, we can watch them for clues.

In a 2010 paper psychologist James Anderson of the University of Stirling in Scotland and his colleagues described video footage of an adult female chimp named Rosie and her companions, which lived at the nearby Blair Drummond Safari and Adventure Park, reacting to the death of her elderly mother. Rosie did not eat as much, sleep as soundly or show as much energy as usual for weeks after her mother died, suggesting that the animal may have been in mourning. Other apes, including gorillas in the Democratic Republic of the Congo's Virunga National Park, displayed similar patterns after the death of a parent or a peer.

Behaviors that suggest grief over the death of a relative or close companion have also been observed in dogs, cats and other species ranging from dolphins to ducks [see "When Animals Mourn," by Barbara J. King, on page 100]. It is difficult, however, to determine whether a specific behavior—such as waiting for a companion's return—is an expression of grief or even to what extent various animals can comprehend death.

Grief is not the only complex emotion that animals may feel. Psychologist Frans B. M. de Waal of Emory University and his colleagues have demonstrated that chimps prefer actions that will help peers to those that just benefit themselves, indicating that they are inclined toward altruism—a highly social quality once thought to be the exclusive domain of humans.

Social intelligence, as distinctive and intricate as it is, may not be easily separable from other forms of smarts such as problem-solving ability or knowledge of the world. For example, a scrub jay that moves its food stores to keep them secret has performed both social and nonsocial mental gymnastics, including, Lefebvre says, "sophisticated memory mechanisms and time travel [that project] future needs for food." Yet although brilliance very likely has multiple facets, social cunning is one important—and often underappreciated—element. Indeed, the smarter we humans become about assessing the social intelligence of animals, the more closely related to us they may seem. SA

Katherine Harmon Courage is a contributing editor at *Scientific American*. Her first book, *Octopus! The Most Mysterious Creature in the Sea* (Current/Penguin, 2013), examines that animal's famed intelligence, among other astounding traits.

MORE TO EXPLORE

Elephants Know When They Need a Helping Trunk in a Cooperative Task. Joshua M. Plotnik et al. in *Proceedings of the National Academy of Sciences USA*, Vol. 108, No. 12, pages 5116–5121; March 22, 2011.

Monkeys Represent Others' Knowledge but Not Their Beliefs. Drew C. W. Marticorena et al. in *Developmental Science*, Vol. 14, No. 6, pages 1406–1416; November 2011.

Theory of Mind in Dogs? Examining Method and Concept. Alexandra Horowitz in *Learning and Behavior*, Vol. 39, No. 4, pages 314–317; December 2011.

Social Cognition. Robert M. Seyfarth and Dorothy L. Cheney in *Animal Behavior*, Vol. 103, pages 191–202; May 2015.

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WHEN ANIMALS ACCIDENTALLY ATTACK

Every so often a critter takes a shot at making headlines **By Steve Mirsky**

IN JOURNALISM, there's what you call your dog-bites-man situation. Which is anything too common and expected to be a good story (unless the dog is one of those *Resident Evil* hellhounds, or the man is Cesar Millan). An example of a dog-bites-man science story is yet another confirmation of Einstein and relativity.

Then there's your more compelling man-bites-dog scenario. Which is something out of the ordinary (unless the man is competitive eater Joey "Jaws" Chestnut, and the dog is a Nathan's Famous). An example of a man-bites-dog science story was the 2011 claim of neutrinos that move faster than light. Turned out they do not. Clocks got blamed, which is appropriate because part of the experiment was in Switzerland and the whole thing was cuckoo.

Every so often, however, we are treated to a dog-shoots-man story. Which is when a dog shoots a man.

An exemplary dog-shoots-man incident occurred on November 27, 2011, when a Utah duck hunter left his 12-gauge shotgun unattended in his boat. The victim got out of the boat to adjust the decoys, at which time his dog allegedly stepped on the gun, causing it to discharge a literal butt-load of pellets—to add injury to insult, 27 pellets wound up in the man's buttocks.

Initial reports noted that neither the dog nor any ducks were injured. If the gun's safety was on, the dog would have had to disengage it, which would elevate this shooting from a crime of negligence to a crime of intent, if anybody was going to charge the man's-former-best-friend.

No one has ever accused a cat of being man's best friend, especially if that man caught a bullet meant for a feral feline. Such a cat-man-duo was the subject of a 2012 news article out of the otherwise bucolic town of Yacolt, Wash. The perpetrator-cum-victim intended to shoot a cat that had been hanging around his house, *The Columbian* newspaper reported. The man "was attempting to load a .22-caliber, semiautomatic rifle when it discharged into his foot." Given that he was going to need nine accurate shots to fully and finally dispatch the cat, perhaps he should consider himself lucky he got shot only once. Let's hope he could other-foot the hospital bill.

Such cat and dog stories may be rare, but deer on the verge of becoming venison seem to even the score with hunters regularly, as evidenced by the results of an Internet search for "deer shoots hunter." A dead animal's reflexive kick that finds a trigger seems to be a common method of postmortem revenge, which for the wounded party can only be described as cold comfort.

Although we inkjet-stained wretches gravitate toward animal-shoots-human stories, I learned early on to be wary. I got my lesson back in 1992, when I heard a radio report about a Missouri man who was allegedly shot by a wild turkey. The hunter was said to have bagged the bird, after which he tossed both it and his gun into the trunk of his car. The hunter's son later opened up the trunk, and the turkey, merely stunned, thrashed around, clawed the trigger and shot the victim—well, the second victim—in the dark meat, I mean, thigh.

A DEAD ANIMAL'S REFLEXIVE KICK THAT FINDS A TRIGGER SEEMS TO BE A COMMON METHOD OF POSTMORTEM REVENGE.

Embarking on my own coverage of this important story, I called the Missouri Department of Conservation. At which point an agent told me that the turkey-did-it version "wasn't brought up until quite a bit after we took statements from the people involved. It almost boils down to a joke." He also strongly intimated that investigators suspected that the hunter's son was at fault. Which, if true, would have made for a stressful dinner at that house, as both turkey and wound got dressed.

Fortunately, the turkey and duck hunters healed, and the dog may heel. (The cat was fine and will never heel.) Which means their license fees can continue to support game management efforts and habitat maintenance. I just recommend hunting with a trusted human—if he sees your dog go for your gun, he can yell, "Duck!" SA

Steve Mirsky has been writing *Scientific American*'s humor column, Anti Gravity, since atmospheric carbon dioxide levels were about 358 parts per million. He also hosts the magazine's podcast Science Talk.

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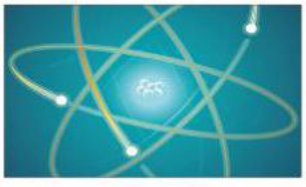

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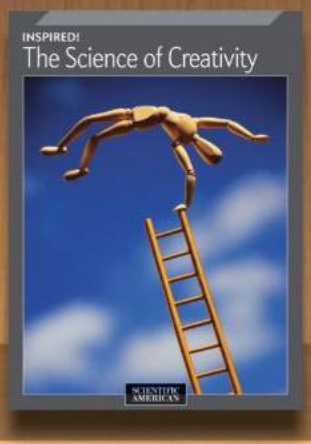

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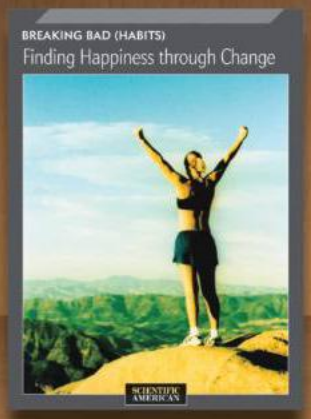

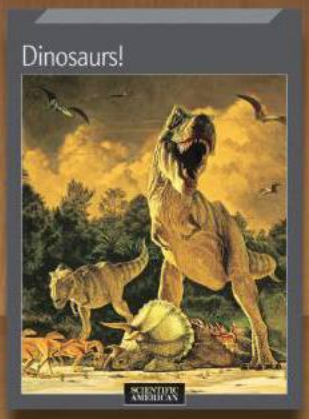

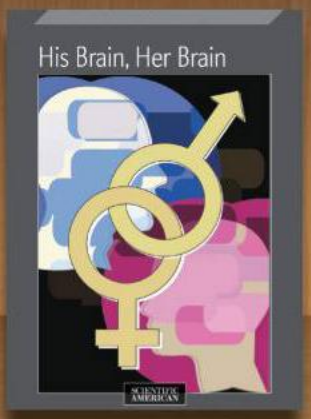

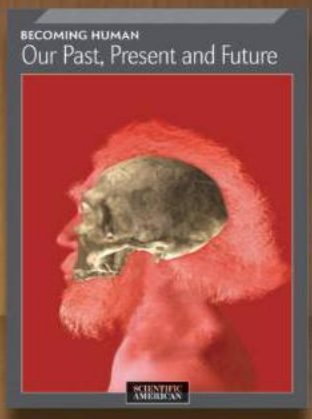

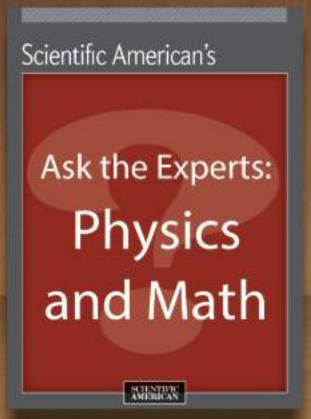

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